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CLASSIFICATION OF ROOT SYSTEMS OF FORBS OF GRASSLAND AND A CONSIDERATION OF THEIR SIGNIFICANCE

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Plants other than grasses constitute an important part of the native grasslands of North America. Most of these are forbs, a few are shrubs and half-shrubs. Probably 85 to 90 percent of the forbs are perennial and most are as deeply rooted and many far more deeply rooted than the grasses. Their number varies considerably from place to place. In the prairie of the central part of the North American Lowland and on the hard lands and sandy soils of the Great Plains they compose, perhaps, between 5 and 15 percent of the vegetation. They are least abundant in the drier habitats.

A recent summary of the community root habits of grasses and an interpretation of the findings included a discussion of soils and climate of each of these extensive areas (Weaver 1958). Hence this need not be repeated here. Suffice it to say that in mixed prairie westward the drier air and decreased water content of soil become limiting factors for growth. Forbs decrease gradually in number, size of individuals, and in the extent of their groupings in societies. This condition prevails despite the fact that the more mesic species of prairie are largely replaced by more xerophytic ones of the Great Plains.

Forbs accommodate themselves not only to the climate but also to the environment imposed upon them by the grasses. On lowland prairie most forbs are tall. They grow even more rapidly than the grasses and may for a long time or continuously overtop them. Many other species flourish on upland true prairie where they form extensive societies. Much competition occurs between grasses and forbs, not only for light but also for water and nutrients. Roots of most grasses occupy only the first 4 to 6 feet of soil. Usually forbs are more deeply rooted. Their roots have rates of growth not unlike those of grasses and depths of 3 to more than 4 feet may be attained during the first growing season and 8 to 15 feet at maturity. Hence, they may absorb partly below the root zone of grasses and thus lessen root competition. Perhaps 90 percent of the abundant forbs, like most prairie grasses, are not only perennial but have a life span extending over a long period of years.

The root habits of a large number of species of forbs have been examined during a period of several years throughout a wide territory from western Iowa, through Nebraska and Kansas, to the mountains of Colorado. Nearly all of the root systems studied were those of mature perennial plants, undisturbed by grazing. Nearly always 3 to 8 plants of a species were examined. Drawings were made simultaneously with the excavating of the roots and always to exact measurements. In the drawings the roots were arranged as nearly as possible in their natural position in a vertical plane. At each examination the work extended over a field sufficiently large, sometimes several square miles in extent, so that the effects of any local differences in soil texture or structure were largely eliminated.

GROUPS OF FORBS BASED UPON THE NATURE OF THEIR ROOT SYSTEMS

An examination of results shows that the root patterns fall naturally into rather distinct groups. This grouping clarifies a confusion of details and furnishes a logical basis for considering the general root development in relation to the environment as modified by the presence of extensive stands of competing grasses.

Group I

Plants in the first group are characterized by a taproot with widely spreading branches which arise mostly in the first three feet of soil and penetrate deeply. There is relatively little or no provision for much absorption in the surface foot

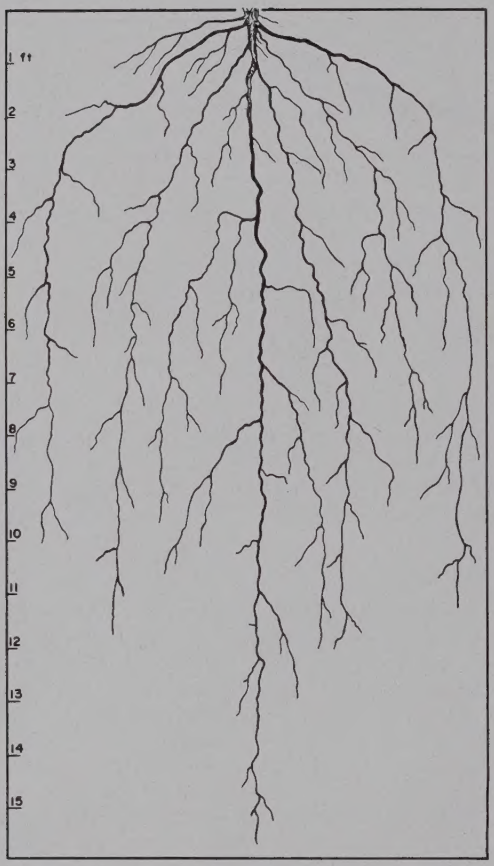


FIG. 1. Root system of blazing star (*Liatris punctata*).

of soil. This root type is well exemplified by blazing star (*Liatris punctata*)[1] in Figure 1.

Table I shows the depth, lateral spread, and general distribution of the species in group I. Column 1 gives the usual depth of penetration in feet; column 2 shows the lateral spread (the radial distance to which roots spread from the base of the plant); and the letters indicate their general distribution in true prairie (P), mixed-prairie hard lands (M), or mixed-prairie sand (S).

The last species in Table I requires explanation. The greatly enlarged taproot of bush morning-glory is often 12 or more inches in diameter in the second and third foot of soil. More slender taproots, 3 to 5 inches thick, may maintain their width to 4 feet. At depths of 4 to 5 feet the taproot often breaks up into a large number of deeply penetrating branches. Lateral spread of branch roots, mostly horizontal in the first 5 feet, is enormous; they run off to distances of 15 to 25 feet or more.

[1] Nomenclature of forbs follows Gleason's New Britton and Brown Illustrated Flora (1952) or Harrington's Manual of the Plants of Colorado (1954).

TABLE I. Depth and lateral spread in feet and general distribution of species in group I. (See text for explanation of symbols in last column)

1. *Argemone platyceras*..... Prickly poppy	12	2	M
2. *Astragalus crassicarpus*... Ground plum	7-12	1.5	PM
3. *Astragalus drummondi*.... Drummond vetch	4-5	3	M
4. *Astragalus gracilis*..... Slender loco	4-5	1.5	M
5. *Eriogonum microthecum*... Slenderbush eriogonum	8-10+	2.5	MS
6. *Glycyrrhiza lepidota*..... Licorice	10-13+	2-3	P
7. *Haplopappus spinulosus*.. Cut-leaved goldenweed	4.5-5	1.5	M
8. *Kuhnia eupatorioides*..... False boneset	12-17	1.5	PM
9. *Lespedeza capitata*..... Bush clover	7-8	2.5	P
10. *Liatris punctata*..... Blazing star	11-16	3.5	PM
11. *Oenothera latifolia*..... An evening primrose	7-9+	3	MS
12. *Petalostemum candidum*... White prairie clover	6-7	1.5	PM
13. *Petalostemum purpureum*. Purple prairie clover	6-8	1.5	PMS
14. *Petalostemum villosum*.... Hairy prairie clover	4-5	2.5	S
15. *Psoralea tenuiflora*..... Psoralea or scurfpea	7-14	1-2	PM
16. *Ratibida columnifera*..... Prairie coneflower	3.5	1	PM
17. *Ipomoea leptophylla*..... Bush morning-glory	9-10+	25+	S

Drawings made to scale of any of the roots of plants 1 to 16 when superimposed on that of the blazing star show great similarity in general pattern. Many of these together with photographs may be found in "The Ecological Relations of Roots" and "Root Development in the Grassland Formation" (Weaver 1919; 1920). In none do the roots extend laterally more widely, and only those of false boneset (*Kuhnia eupatorioides*) penetrate deeper.

Plants of *Astragalus gracilis, Glycyrrhiza lepidota* and *Oenothera latifolia* are sometimes connected by underground parts.

Plants in this group probably absorb mostly from depths greater than those most densely occupied by the roots of grasses. At least their effect upon the grass is usually not marked except where they occur in unusually dense stands. False boneset and bush morning-glory are exceptions. Grasses beneath these plants are shaded out by the dense foliage. To occupy the soil below the grass, roots must extend deeply. In lowlands of true prairie the grass roots are coarsest, least branched,

but deepest. Those of big bluestem (*Andropogon gerardi*) extend downward 7 feet. On upland prairie the grass roots are moderately fine, profusely branched, and 4 to 5.5 feet deep. Grasses of the hard lands of mixed prairie have the finest and most profusely branched roots. They are usually 4 to 5 deep (Weaver 1958).

This type of root system, which is the most common one to most of us, was found on only about one-fourth of 65 species examined. Type I occurs widely in both true prairie and plains hard lands and is often found in sandy soil.

Group II

In the second group, plants have taproots with maximum spread of abundant laterals in the surface 1 to 2 feet of soil where extensive branching provides for much absorption (Table II). Broom snakeweed (*Gutierrezia sarothrae*) and hairy golden aster (*Chrysopsis villosa*) are representative species (Figs. 2 and 3). Fringed sage (*Artemisia frigida*) and broom snakeweed are plants with woody bases but they are grouped here for convenience.

TABLE II. Depth and lateral spread in feet and general distribution of species found in group II

1. *Artemisia canadensis*..... Canada sage	7-8	2.5	MS
2. *Artemisia frigida*..... Fringed sage	6-8	1.5	M
3. *Chrysopsis hispida*..... Rough golden aster	8-10	3	MS
4. *Chrysopsis villosa*..... Hairy golden aster	10-13	2.5	MS
5. *Eriogonum jamesii*..... James eriogonum	7-9	3	M
6. *Grindelia squarrosa*..... Gumweed	5-6	2.3	M
7. *Gutierrezia sarothrae*..... Broom snakeweed	5-7	1.5-2	M
8. *Penstemon haydenii*..... Hayden penstemon	2.5-3	2	S
9. *Thelesperma megapotamicum*..... Greenthread	3-3.5	3.3	MS
10. *Verbena stricta*..... Woolly verbena	4-5	1.5	M
Subgroup without taproots			
11. *Opuntia comanchica*..... Prickly pear	2-3	5-6	M
12. *Tradescantia virginiana*... Virginia spiderwort	1.5-2	3	SP
13. *Tradescantia occidentalis*.. Prairie spiderwort	1.5-3	1.5	SPM
14. *Commelina virginica*..... Virginia dayflower	2-3	2.3	SPM
15. *Yucca glauca*..... Small soapweed	6-7	32	MS

Only 1 of the 10 species has the great depth of penetration common to 8 species in group I. Spread of lateral roots is about the same. The chief difference is the placement of most of the root system in the upper portion of the soil in direct competition with the roots of grasses and sedges.

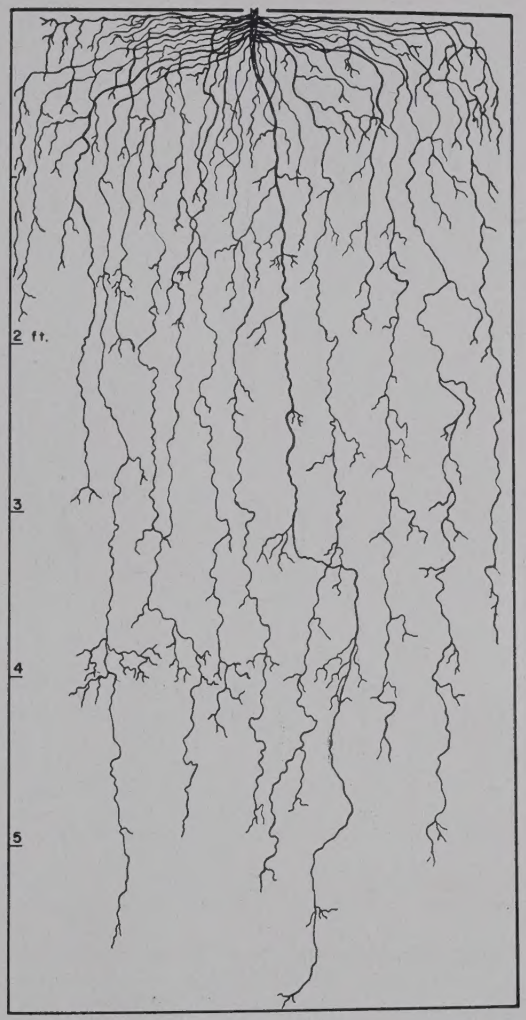


FIG. 2. Root system of broom snakeweed (*Gutierrezia sarothrae*). Redrawn from "The Ecological Relations of Roots."

A few species without taproots but with root systems confined largely to the surface soil where they spread very widely and compete extensively with the grasses are included in Table II. Cacti, as is well known, are among the most abundant plants of the Great Plains. *Opuntia camanchica, O. fragilis,* and *O. polyacantha* have been examined.

The root system of the first species, for example, was almost confined to the first 3 inches of soil. The widely spreading and somewhat fleshy roots furnished an enormous surface absorbing

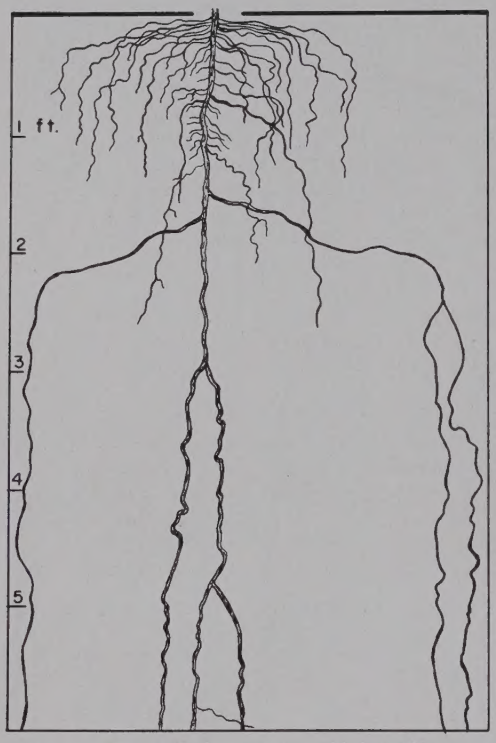


FIG. 3. Upper half of root system of hairy golden aster (*Chrysopsis villosa*). The lower half had only four fine branches. Redrawn from "Ecological Relations of Roots."

system. Only 4 to 6 roots, moderately branched, extended downward and attained depths of 2 to 3 feet.

The spiderworts and dayflower, all with somewhat fleshy roots, are also so shallowly rooted that they compete for water and nutrients directly with the grasses. Small soapweed, a coarse evergreen plant, does not possess a taproot. The caudex or woody base, 3 or more inches thick, often penetrates downward 2 feet or more or extends outward or obliquely downward. From these stems arise a profusion of slender fleshy roots. These extend outward, mostly horizontally, for distances of 25 to 32 feet. Thus, roots are extremely abundant in the upper 3 feet of soil; others extend downward several feet.

The entire group of 15 species includes nearly one-fourth of the forb population under consideration. All of these occur most abundantly and many only in the hard lands and sandy soil of mixed prairie. Both species of sage become extremely abundant as the vigor of grasses declines under overuse of the range. Broom snakeweed and gumweed behave in a similar manner. Small soapweed and cacti also thicken their stand somewhat in the degree that the western ranges are overgrazed. Woolly verbena and gumweed occur only as weeds in the area occupied by true prairie.

The clay loams, silt loams, and sandy loams of the Great Plains are designated as hard land to distinguish them from sand, which is of common occurrence. These soils become so compact when dry that often a pick is necessary in making a trench for root studies. The grasses, like the forbs of this group, spread their roots widely and form dense masses in the surface soil. The very abundant deeper grass roots are also well furnished with branches. All the grasses are very drought resistant. They can undergo repeated dormancy in drought and revive again when soil water is available. The moderately fine but widely spread roots of sand-hill grasses reach depths of about 4 to 7 feet. The growth of vegetation in both true and mixed prairie occurs throughout the summer, but in sand, as on hard lands, it is somewhat according to the occurrence of rain (Weaver 1958).

Group III

A third group includes plants with taproots or several main roots which produce relatively few or no branches but penetrate deeply. When branches occur they are usually from the deeper part of the root system (Table III). Examples of the type are bractless mentzelia (*Mentzelia nuda*), narrow-leaved four-o'clock (*Mirabilis linearis*), and pale purple coneflower (*Echinacea pallida*) (Fig. 4).

Plants of species numbers 2, 3, 6, 8, and 12

TABLE III. Depth in feet and general distribution of species in group III

1. *Abronia fragrans* Snowball sand verbena	3.5—4	MS
2. *Asclepias arenaria* Sand milkweed	8-11	SM
3. *Baptisia leucophaea* False indigo	7-8+	P
4. *Echinacea pallida* Pale purple coneflower	6-8	PM
5. *Lithospermum incisum* Narrow-leaved puccoon	8-10	PM
6. *Lygodesmia juncea* Rush skeletonplant	10-21+	PM
7. *Mentzelia nuda* Bractless mentzelia	4-5	S
8. *Mirabilis linearis* Narrow-leaved four-o'clock	4—5.5	M
9. *Oxytropis lambertii* Crazyweed	10-12	M
10. *Psoralea argophylla* Silver-leaf psoralea	6-8	PM
11. *Sphaeralcea coccinea* Scarlet globemallow	8-13	M
12. *Silphium laciniatum* Compassplant	9-14	P

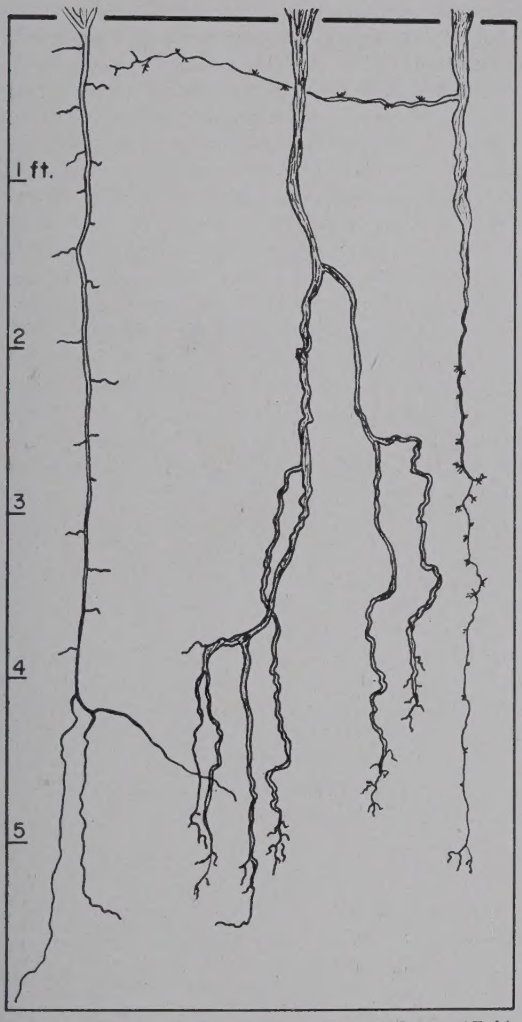


FIG. 4. Root systems of pale purple coneflower (*Echinacea pallida*) (left), bractless mentzelia (*Mentzelia nuda*) (center), and narrow-leaved four-o'clock (*Mirabilis linearis*) (right). Plants are from true prairie, sand hills, and plains hard lands, respectively. Redrawn from "Root Development in the Grassland Formation" and "Ecological Relations of Roots."

have fleshy roots. Those of *Silphium laciniatum* were of largest size, often 1 to more than 2 inches thick. This rosinweed gives rise to a few large laterals and some small ones in the deeper soil. In mixed prairie, *Lygodesmia juncea* sometimes produces a few unbranched laterals which closely resemble the main root.

This root type is well represented in both true and mixed prairie and somewhat less so in sand. Plants range from moderately to very deeply rooted. The 12 species in this group compose nearly 20 percent of the 65 species of forbs examined. Only two are particularly harmful to the cover of grass. These are false indigo (*Baptisia leucophaea*) and compassplant (*Silphium laciniatum*). The first has a bushy top near the soil surface which shades the grasses until midsummer, after which the stem usually breaks near the ground line and the top is blown away. Old specimens of compassplant consist of a large clump with many stems and numerous, strong, deep roots. Such plants exclude other vegetation over an area of several square feet.

Roots of plants in this group probably absorb water throughout their entire depth. The fleshy roots shrink rapidly when exposed to dry air.

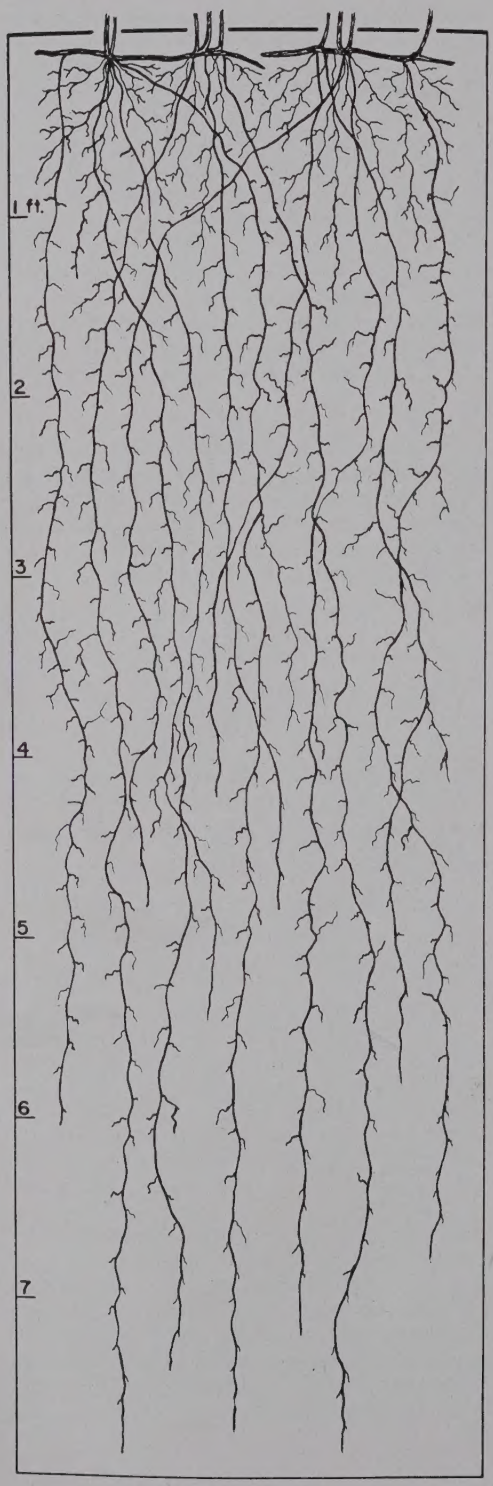
Group IV

A fourth group includes forbs with rhizomes, root offshoots, or corms with numerous main roots of about equal size. Lateral spread is often indefinite (Table IV). An example is many-flowered aster (*Aster ericoides*) (Fig. 5).

Individual plants of lance-leaved psoralea (*Pso-*

TABLE IV. Depth in feet and general distribution of species in group IV

1. *Ambrosia psilostachya* Western ragweed	5-6	M
2. *Antennaria neglecta* Prairie cat's-foot	3-4	P
3. *Asclepias pumila* Plains milkweed	3-4	M
4. *Aster ericoides* Many-flowered aster	7-8	PM
5. *Equisetum laevigatum* Smooth horsetail	6-8	P
6. *Helianthus laetiflorus* Stiff sunflower	7-8	P
7. *Lathyrus polymorphus* Peavine	3-4	SM
8. *Liatris scariosa* Tall gayfeather	3-4	PM
9. *Liatris squarrosa* Gayfeather	2.5-3	PMS
10. *Oenothera serrulata* Tooth-leaved primrose	4-5	PMS
11. *Penstemon ambiguus* Gilia penstemon	8-10	SM
12. *Penstemon angustifolius* Narrow-leaved penstemon	5-6	SM
13. *Polygonum coccineum* Smartweed	7-8	P
14. *Psoralea lanceolata* Lance-leaved psoralea	8-10	S
15. *Salvia pitcheri* Pitcher's sage	7-9	P
16. *Solidago canadensis* Canada goldenrod	9-11	PM
17. *Solidago missouriensis* Missouri goldenrod	7-11	PM
18. *Solidago mollis* Velvety goldenrod	7-8	M
19. *Solidago rigida* Stiff goldenrod	5-6	PM
20. *Vernonia baldwini* Baldwin's ironweed	11-12	PM



ralea lanceolata), which may be a few inches to several feet apart, are connected by a more or less horizontal system of underground parts which varies in depth from 2 inches to more than 2 feet. It may extend outward distances of 10 to more than 40 feet. At various intervals along its course new plants arise. Strong, vertically descending roots arise from these underground parts, often at some distance from the erect stems.

Many plants in this group penetrate as deeply as those with strong taproots. Others are less deeply rooted. They are about equally distributed in true prairie and mixed-prairie hard lands, with smaller numbers occurring in sand. This is the largest of the four groups and composes about 30 percent of the species examined. All absorb vigorously in the surface soil and are strong competitors of the grasses. Some of the most abundant and worst weeds in native pastures derived from true prairie are the various goldenrods, many-flowered aster, Baldwin's ironweed and western ragweed. Certain goldenrods and western ragweed are also abundant weeds of western ranges.

The root system of only one perennial forb was encountered in the grasslands that did not fit well in any of the four groups. This was *Euphorbia robusta*. It developed a strong taproot which extended 8 feet into the hard-land soil. No long laterals were developed. Short ones were abundant below 2 feet to the root end.

Significance of the Types in Relation to Grasses and Climate

An examination of the four types of root systems suggests that two of these may have resulted from a long adjustment to competition with the roots of grasses. In group I there is little provision for absorption where roots of grasses are most abundant in the upper part of the solum. In group III absorption at the upper levels of the grass roots is certainly not emphasized by the unbranched or poorly branched but very deep taproots. Group IV with a general distribution of many main roots throughout the soil competes strongly with the grasses. But forbs with taproots and maximum spread of abundant and extensively branched laterals in the upper soil (group II) afford the greatest competition in dry climates. Moreover, nearly all species in this group occur in the drier western soils watered mostly by light summer rains. What are the root habits of forbs in relation to grasses in prairie with light and mostly winter rainfall? Fortu-

Fig. 5. Root system of many-flowered aster (*Aster ericoides*).

nately, the root systems of many individuals of the most important species of grassland in the Pacific Northwest were examined before all of the Palouse Prairie was plowed (Weaver 1915).

The part of this grassland that was examined occurred on Northern Chernozem soil at latitude 47° N. and at an altitude of about 2,300 feet. The mean annual precipitation is 21 inches, less than a fourth of which falls during summer. The friable, dark brown, silt loam is deep and very fertile. Both soil and subsoil are extremely retentive of moisture. This soil may be compared with a gigantic reservoir replenished during fall, winter and spring but thoroughly emptied of its water during summer. Two years of soil sampling to a depth of 6 feet substantiate this statement. In early summer the upper part of the soil loses all of its water available for plant growth, and the entire soil to a depth of 5 or more feet gradually loses most of its available supply to transpiring plants during the summer.

Several of the chief grasses, such as Idaho fescue (*Festuca idahoensis*), June grass (*Koeleria cristata*), and Sandberg bluegrass (*Poa secunda*), are only 12 to 28 inches tall and their roots penetrate only the upper 1.5 to 2 feet of soil. They are cool-season bunch grasses which flower early and become dormant in late June or July. In fall they renew growth, remain green during the mild winter, and develop rapidly in spring. The chief mid grass is bluebunch wheatgrass (*Agropyron spicatum*), also a cool-season species, and its variety *inerme,* now designated as *A. inerme.* Bunches of these wheatgrasses are often 10 inches in diameter, and height is about 3 feet when blossoming occurs in June. Roots do not spread widely in the surface soil, and despite the root depth of 4 to 5 feet, the plants dry early in July. Renewing growth in autumn, they remain green in winter.

In this rather dense cover of grasses, various forbs were plentiful. But with the increasing stress of drought after midsummer the landscape of dry grasses also included the leaden color of many dried, even if deeply rooted, forbs. Only a few sparsely spaced goldenrods, asters, and goldenweed continued to blossom. Late maturing species were not abundant.

Depth and spread of 12 forbs are shown in Table V. All belong to group I. There was little or no provision for much absorption in the surface foot of soil. All, except *Potentilla blaschkeana,* had strong taproots. It produced 2 to 5 main roots from a short thick crown.

No plant of group II, with taproot and maximum spreading of branches in the surface foot, was found. Only one species, the carrot-like *Leptotaenia multifida,* had a fleshy taproot. It penetrated deeply (5.5 feet) and had relatively few branches (group III). Plants of two species possessed rhizomes and many small roots of about equal size which reached depths of 5 to 7.5 feet (group IV). These were *Hieracium scouleri* and *Sieversia ciliata.*

TABLE V. Depth and lateral spread in feet of forbs of Palouse Prairie

1. *Astragalus arrectus*[2]. Milk vetch	4-6	2
2. *Balsamorhiza sagittata*. Arrowleaf balsamroot	5.5-9	3
3. *Geranium viscosissimum*. Sticky geranium	5-9	3
4. *Helianthella douglasii*. Douglas helianthella	4.5-5	2
5. *Hoorebekia racemosa*. Goldenweed	5.5-11	2
6. *Heuchera glabella*. Alumroot	5-6	1.5
7. *Lithospermum ruderale*. Wayside gromwell	5-6	2.3
8. *Lupinus leucophyllus*. Velvet lupine	5-5.5	3
9. *Lupinus ornatus*. Ornate lupine	7-11	4
10. *Potentilla blaschkeana*. Blashke cinquefoil	6-7.5	1
11. *Sidalcea oregana*. Oregon checkermallow	3-4	1
12. *Wyethia amplexicaulis*. Mulesear wyethia	5-6	4

[2]Nomenclature follows Piper and Beattie's Flora of Southeastern Washington and Adjacent Idaho (1914).

A comparison of the community root habits of vegetation under winter precipitation but similar in amount to that of parts of the Great Plains suggests the conclusion that the plains root habit of forbs in class II is a response to dry soil and light summer showers. *Bouteloua gracilis, Buchloe dactyloides* and *Agropyron smithii,* which grow both in mixed prairie and the drier parts of true prairie, develop widely spreading, shallow roots only in the plains. Moreover, there is some evidence that *Grindelia squarrosa* and *Gutierrezia sarothrae* have a more poorly developed surface absorbing system in parts of the plains with the highest rainfall. In true prairie plants seldom develop the widely spreading, superficial laterals so characteristic of many plains species. This may result from the greater and usually continuously available water content in prairie soil.

Six of the most deeply rooted plants found in this study occurred in true prairie. They were numbers 6, 8, 10 and 15 of Table I and two half-shrubs, *Amorpha canescens* (8-17 feet) and *Rosa suffulta* (12-21 feet), which behave as forbs under annual mowing.

Water Supply for Deeply Rooted Species

In true prairie the parent material below the solum, is almost continuously moist, but not wet, to many feet in depth. Deeply rooted forbs may live largely on the water that penetrates beyond the depth of the grass roots. Many of these are species of legumes. They are always interspersed among the grasses and, even where most abundant, they do not grow in such dense stands as do cultivated legumes. When Prairie soil is broken and alfalfa is grown, its taproots develop rapidly and in a few years reach depths of 30 feet or more. A two-year-old meadow in eastern Nebraska has been shown to decrease the water content to depths of 25 feet and a six-year-old one to 33 feet. The excellent growth and high yields during the first 3 or 4 years are almost independent of the amount of rainfall, since the plants are using water stored deeply. But unlike native forbs they absorb the available water so completely that new crops of alfalfa cannot be produced on the same soil, since the deep soil is not again moistened during a very long period of years (Kiesselbach *et al.* 1929).

The character of the root system is usually an indicator of soil conditions. There is no substantial evidence of root penetration of plains forbs into soil where water is nonavailable for growth. It has been shown that roots of forbs do penetrate deeply even under the usual relatively light rainfall of the Great Plains (12-23 inches).

It is common knowledge among students of soils that in unusually wet years the soil of the High Plains may become wet to depths of 5 to 6 feet (Weaver and Albertson 1956, Albertson *et al.* 1957). Direct proof that water penetrates much deeper in places is afforded by the fact that wet soil was found in several trenches; in many instances even the deepest roots were taken from moist soil. The answer to the problem of deep water penetration under the rather light rainfall of the Great Plains seems to lie in soil disturbance.

"Ground squirrels, gophers and badgers dig and burrow deep into the earth. Harvester ants channel and loosen soil. Of scores of trenches dug in excavating roots of the prairie plants scarcely one was free from the work of recent or ancient soil excavation and refilling. Prairie dogs ranged nearly throughout the mixed prairie. They dig deeply, often to 12 or even 15 feet, and place enormous quantities of soil upon the land surface. Moreover, coarse, deep taproots upon their death and decay leave holes, curbed by soil compressed in their growth and expansion, which remain open, except perhaps at the top, a very long time. When prolonged periods of drought occur, as they did in the early 1890's and in the recent 1930's, very deep cracks and fissures 1 to 2.5 inches wide result from the shrinking of the soil. Such periods are followed by heavy rains, little water penetrating the nearly bared and dust-covered parched soil. Large volumes of water sink through the cracks and, locally at least, thoroughly wet the deep soil. When the cracks are again closed, water is lost very slowly but permits deep root penetration" (Weaver and Albertson 1956).

Soil fissures and cracks often occur at intervals of 6 to 12 feet and precipitation following extended periods of drought is sometimes three or four times the usual amount. Not infrequently the darker colored top soil was revealed in trench walls to a depth of several feet where it had been deposited in fissures by runoff water. Such differences in soils have marked effects upon root penetration and branching. When a root enters the softer soil of a filled crack or ancient burrow it usually extends much deeper and branches more profusely than other roots of the same forb or grass. In fissures differences in root depth, compared with that of surrounding vegetation, may be measured in feet. Even earthworm burrows greatly affect root extent, especially in semiarid lands. Sometimes, as in Palouse Prairie, the burrows are one-fourth inch wide and some are 10 feet in depth. Differences in soil structure at various levels in the soil profile and not uniformity is the rule in soils of the Great Plains. These result not only in variations in water content but also in nutrients. Root tubercles on native legumes are very irregularly distributed. On roots of *Psoralea lanceolata,* for example, branching was profuse and nodules were abundant only in the seventh to ninth foot of soil. On *Amorpha canescens* they occurred irregularly to a depth of 16 feet. It has been observed that in pockets of fine sand and silt abundant root branching often occurs while in adjacent layers of moist sand and gravel few or no branches are produced. Often the cause is differences in availability of nutrients.

Root Habits and Response to Drought

The response of forbs to the great drought of 1933-40 was closely related to their root habits. In midsummer of 1934 upland grasses of true prairie had wilted and dried when no available water occurred to depths of about 4 feet. This was also the fate of certain shallowly rooted forbs. Deeply rooted plants remained green and many blossomed, although somewhat earlier than usual. All types of root systems were represented, except II, in this drought-resistant group. In ravines where most lowland grasses finally lost their

green color and were partly dried, deeply rooted forbs, although dwarfed, remained green. Thus, the persistence of forbs during the years of drought was remarkable. But with decreasing amounts of available soil moisture and extremely unfavorable aerial environment they slowly succumbed. In true prairie west of the Missouri River losses were approximately one-half to two-thirds of the forb population.

In both true and mixed prairie the more deeply rooted forbs persisted for several years. In mixed prairie only about 17 species of native perennials remained after 3 or 4 years. Excepting cactus, these were then reduced to about 10 species, none of which belonged to class II. But near the end of drought (after 1939) only *Sphaeralcea coccinea, Kuhnia eupatorioides, Psoralea tenuiflora,* and *Cirsium undulatum* could be found after prolonged searching in favored spots; the rest were seen rarely (Weaver and Albertson 1943). These plants with very deep taproots had existed on moisture available only far below the subsoil over a long period of time.

In true prairie the upper 3 to 4 feet of several forbs have been encased experimentally in such a manner that they could not absorb. During two summers the plants grew normally (Nedrow 1937). Water and probably nutrients were obtained beneath the solum. During the last years of drought a dry layer of soil, with no water available for growth, occurred between depths of 2.5 and 5 to 5.5 feet. Thus, part of the deep taproots were unable to absorb in this layer, yet many remained alive.

Summary

Root systems of several plants of each of 80 species of forbs were examined and classified. Sixty-five grew among the grasses in true prairie of western Iowa and eastern Nebraska and in the hard lands or sand in mixed prairie of Kansas, Nebraska and Colorado.

The root systems were of four types. About 25 percent developed taproots with widely spreading branches which arose in the first 3 feet of soil and penetrated deeply, with little or no provision for much absorption in the surface soil (blazing star—*Liatris punctata* type). A second group had taproots with maximum spread of abundant laterals in the surface 1 to 2 feet where extensive branching provided for much absorption (broom snakeweed—*Gutierrezia sarothrae* type). With a subgroup of cacti and several monocots with similar surface-absorbing but fibrous roots, this group also composed 25 percent of the total. A third group (pale purple coneflower—*Echinacea pallida* type) consisted of plants with taproots or several main roots which produced relatively few or no branches but penetrated deeply. It composed 20 percent. Forbs with rhizomes, root offshoots, or corms and with numerous main roots of about equal size (many-flowered aster—*Aster multiflorus* type) made up the remaining 30 percent.

There is considerable evidence that the broom snakeweed type represents an adaptation to secure water from light showers in the dry plains soil. Plants of this group were rarely found in the other prairies.

Most roots of the blazing star type absorb to great depths, 5 to 12 or more feet, and thus below the general depth of roots of competing grasses. Twelve of 15 forbs in Palouse Prairie had this root type. Plants of the pale purple coneflower group probably compete least with the grasses for water and nutrients. When branches occur they are usually from the deepest part of the taproot. Several species have fleshy roots.

Great competition with grasses occurs in the many-flowered aster type. This group also produces some of the worst weeds of native pasture.

When a root system is assigned to its type, and depth and lateral spread are stated, a fair conception of its appearance may be had with little further description.

The great depth of water penetration in plains soil is considered. Root habits and response of forbs to great drought are discussed.

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VEGETATIONAL CHANGES IN THE CALIFORNIA ANNUAL TYPE

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INTRODUCTION

The objectives of the study were to describe fluctuations in the California annual type that occur within a growing season and from one year to the next. These are given for three sites. Other changes that are related to mulch manipulation, grazing, and fire are discussed.

Not only does this type of information have value in itself but it also has value in the interpretation of studies on the management of the vegetation for forage production. If sampling can be done at one time only, vegetational changes during the growing season necessitate that the sampling date be selected carefully. Otherwise, seasonal differences may be unknowingly confounded with those due to other causes.

That the annual-type vegetation differs greatly in any given place from one year to another is well known. Annual vegetation also changes with season and the pattern may differ from one site to another. The three types of changes are superimposed and must be determined before the effect of manipulation can be accurately evaluated.

The magnitude of these changes was measured in terms of number of plants per unit of area on plots located on the Hopland Field Station in Mendocino County. The results, therefore, are from a restricted area and are presented as such. They are not offered as norms to describe the "average California annual type." However, the principles found are in essential agreement with the work of others. Together they may be interpreted as giving the basic sequences and directions of change. It is assumed that these sequences are not fortuitous and that they would show a significant relation to those of other areas and years despite diversities between individual situations.

The term "California annual type" is used in this paper to denote that vegetation in California which is composed primarily of annuals. The type is a mixture of many species of grasses and broad-leaved herbs, and species that are native and introduced. Although many perennial species are present, individual perennial plants are scarce. The type is located below the 4,000 foot level in the Central Valley and intermittently in the Coast Ranges. It is the understory in the open areas of oak-woodland and to some extent in the chaparral types. Actually the type is a very broad one. It contains many sub-types which can be delineated by species composition or other characteristics, and related to the differences in soil and climate.

The term "vegetation" is used to signify a group of individual plants growing together. The size of area and complexity of the group is indicated only by the context in which the term appears. The term "vegetational change" is used to specify changes over time in the number of plants per unit of area or in relative species composition on a percentage basis.

Sincere appreciation is extended to members of the Faculty Seminar in Ecology at the University of California who offered many helpful suggestions during discussions of this paper.

METHODS

In early December of 1951, sixteen plots, each 10 feet on a side, were established in a 4 x 4 Latin square at three locations on the Hopland Field Station. This design was used so that location effects in two directions, rows and columns, could be measured and removed statistically from the treatment effects within each study site. Treatments were dates of sampling. The first set of four plots was sampled on an average date of December 7; the second set was sampled on February 6; the third on April 5; and the fourth on June 9. The sampling consisted of counting the number of annual plants by species or groups of species in ten quadrats of one square inch in each plot. The occasional perennial plant was omitted. Sampling was done on all plots at the same time every year.

The square inch quadrat was handled by cutting out a block of soil of that size with the aid of a measuring fork and stiff putty knife. The block was then carefully spread out or pulled apart and the live plants counted as they were discarded. In June all dry individuals were counted but undoubtedly some were missed because they had shattered. A total of 2,400 quadrats were taken in the five years.

The sampling during the fall and winter was on seedlings, when positive identification of all the species was impractical. *Bromus mollis,*[1] *Bromus rigidus,* and *Erodium botrys* were easily identified and recorded separately. The others were grouped either as "other grasses," "legumes," or "other

[1] Botanical nomenclature follows Hitchcock (1950) for grasses and Jepson (1923) for other plants.

broadleaved plants." Legumes were generally few in number and included *Lotus micranthus, Lupinus bicolor, Trifolium bifidum, T. ciliolatum, T. depauperatum, T. microcephalum, T. microdon,* and *T. variegatum.* The list of other grasses included *Aira caryophyllea, Avena barbata, Briza minor, Festuca dertonensis, Gastridium ventricosum, Hordeum hystrix,* and *Poa annua.* The principal other broadleaved plants were *Baeria chrysostoma, Cerastium arvense, Filago californica, Galium parisiense, Hypochoeris glabra, Lepidium nitidum, Linanthus ciliatus, Micropus californicus, Navarretia intertexta, Orthocarpus erianthus, Pentachaeta exilis, Plagiobothrys nothofulvus, Plantago erecta,* and *Spergula arvensis.* The total flora at the three locations numbered about 50 species with some variation from year to year and among the locations.

The Study Sites

Site I was in an area that had been ungrazed by domestic livestock for several years previous to and during the study. However, deer made frequent use of it in the winter months. One result of this protection from domestic animals was that large amounts of mulch were present throughout the five years of the study. Perennials were conspicuous and the common ones were *Elymus glaucus, Melica californica, Koeleria cristata, Achillea millefolium,* and *Eschscholtzia californica.* These were not observed either to increase or to decrease during the five years.

The soil of Site I consists of water-deposited material in a small fan below an extensive area of the Josephine soil series. The surface layer is a sandy loam containing many rock fragments. The reaction is slightly acid and the color is brown to reddish brown. Drainage throughout the soil is good. The exposure is southeast with a slope of about 10 percent. In the winter this area is shaded in the afternoons.

Site II was in a grazed pasture, about one-half mile from where sheep were fed. Grazing was estimated to be moderate. The soil is classed as Sutherlin fine sandy loam. It is 3 to 4 feet in depth with a brown, loamy, slighty acid surface layer which grades into a yellowish brown claypan that is neutral in reaction. Surface drainage is moderate but water moves slowly through the claypan. Occasionally after heavy rains small undulations in the soil surface contain free water for a few hours. No perennials were present. The slope is less than 10 percent toward the south.

Site III was in the same pasture with site II but near where sheep were fed every winter. It was grazed and trampled heavily before 1951. During the course of the study, grazing was still heavy but periods in the winter and spring without grazing allowed the plants to attain more growth than they had in previous years. The soil at this site also is classed as Sutherlin fine sandy loam, but it is only 2 to 3 feet thick, and lighter in color and less friable than at Site II. Surface drainage is rapid. Usually there was a moderate amount of mulch on the soil but it disappeared during each winter. Perennials were absent at the beginning of the study but periods without grazing allowed *Stipa pulchra* to increase during the five years. By 1956 it was numerous on the plots and in the vicinity. The slope is approximately 10 percent toward the southeast.

Normal Seasonal Development of Plants

Following germination and slight growth in the fall there was a period until about the middle of March or the first of April when growth was very slow. Little difference in height of plants could be seen between the December and February sampling dates. Fast growth of the plants was underway or about to begin at the time of the April sampling. All plants were dry by the June sampling time. However, in 1953 and 1956 a few sprigs of *Mendicago hispida* at Site II and a few grass stems at Site I were still green. In those two years a few plants were green under the oak trees in the vicinity of the plots. At Site I, *Bromus rigidus* was usually in the last stage of drying and appeared reddish in contrast to the light tan of the other species. *Aira caryophyllea* and *Briza minor* were the first grasses to mature and *Bromus mollis* was intermediate.

During every winter at Site I the plants were taller, more slender and grew in sparser stands than at the other sites. This was probably the result of large amounts of mulch, both matted on the soil and standing.

Site III was characterized by short plants at all seasons. In December and February few were over one inch in height and by June the vegetation was seldom over one foot in height. This was because the major species were short plants like *Aira, Briza, Gastridium, Trifolium, Erodium* and *Festuca* and there were few plants of *Bromus mollis* and *Bromus rigidus* (Figs. 1-3).

Bromus mollis and *Erodium botrys* gave Site II a characteristic appearance of a mixture of grass and broadleaved species (Fig. 4). In all years except 1954 the ground between these plants was essentially bare of the smaller grasses and broadleaved plants. In 1954 *Briza minor* and *Aira caryophyllea* were common, in 1953 and 1956 *Medicago hispida* was abundant but in 1954 there was none of it, and in 1952 *Gastridium ventri-*

FIG. 1. On February 2, 1955, at Site III the new plants were less than an inch tall and formed a green carpet beneath the dry standing plant material (See Figs. 2-3).

FIG. 2. Same area as Fig. 1 on April 7, 1955. The new plants were little taller but considerable mulch had been removed by grazing and decomposition.

cosum was present. It did not make a conspicuous appearance until June.

Several perennial grasses were present in the plots of Site I and these were always green, and in 1954 still flowering, during the first week of June (Fig. 5).

NUMBER OF PLANTS PER UNIT OF AREA

The number of individual plants on a square inch of soil varied between zero and 91. Average numbers per square inch in sample sizes of 40 varied between 3.3 and 35.0 plants (Fig. 6). Converted to numbers per square foot, these are 475 to 5,040. The maximum calculated from the 91 is 13,104. In another study the number of plants on 4 separate square feet in mid-winter near Site III were 2,746, 3,014, 3,393, and 3,643.

From a study in Madera County, Biswell and Graham (1956) reported as many as 20,875 *Festuca megalura* seedlings per square foot in dense

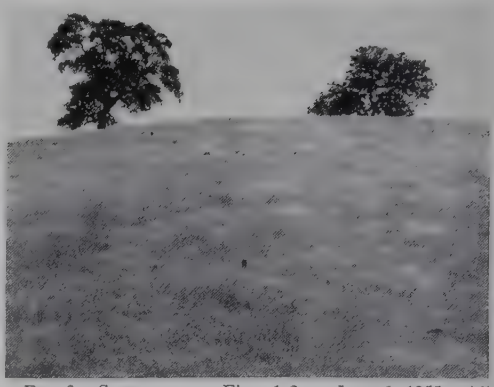


FIG. 3. Same area as Figs. 1-2 on June 6, 1955. All plants had matured at a height of about 6 inches. *Erodium botrys* was conspicuous even though it was overtopped by numerous grasses.

FIG. 4. Site II at it appeared on June 9, 1953. The light colored areas are mostly *Bromus mollis* and other grasses. The dark areas are *Erodium botrys* and *Medicago hispida*.

FIG. 5. Site I on June 6, 1955. The tall annual is *Bromus rigidus* and the large perennial bunch grass is *Elymus glaucus*. The annuals were dry and the seed beginning to fall but the perennial was still green.

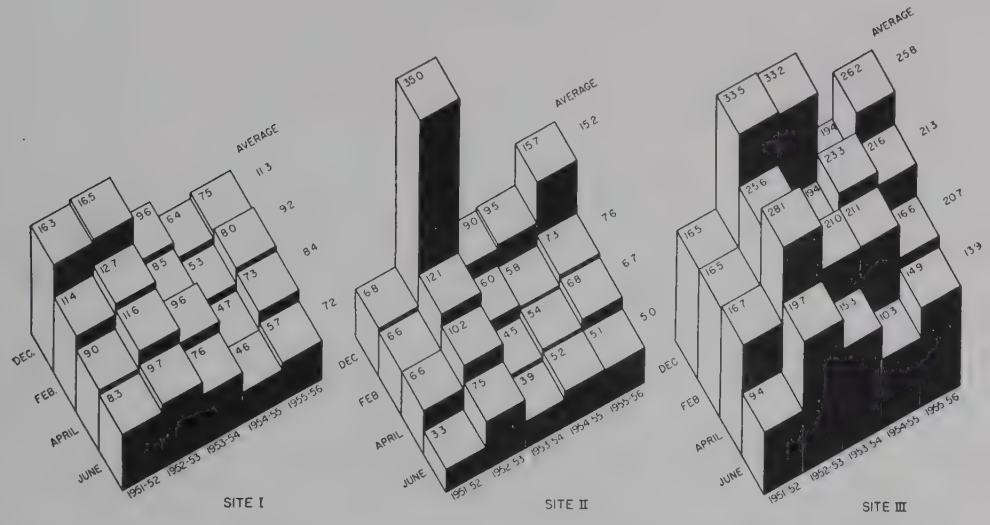


FIG. 6. Average numbers of plants per square inch for all species from a sample size of 40 for four seasons in each of five years.

stands; *Bromus mollis,* 17,433; and *Erodium botrys,* 1,048. In stands of average density dominated by the two grasses at maturity, they found between 1,805 and 7,830 plants of all species. Comparable numbers of mature plants in this study were 475 and 2,837. Reasons for the difference between areas in number of individuals per unit of area are not known.

Much variation in numbers of plants per unit of area occurred locally within but a few inches. The ratio of the standard deviation to the mean was usually between 30 and 40 percent. This indicated that a sample size of 40 should measure differences as small as approximately 10 percent of the means.

CHANGES IN TOTAL NUMBERS FROM DECEMBER TO JUNE

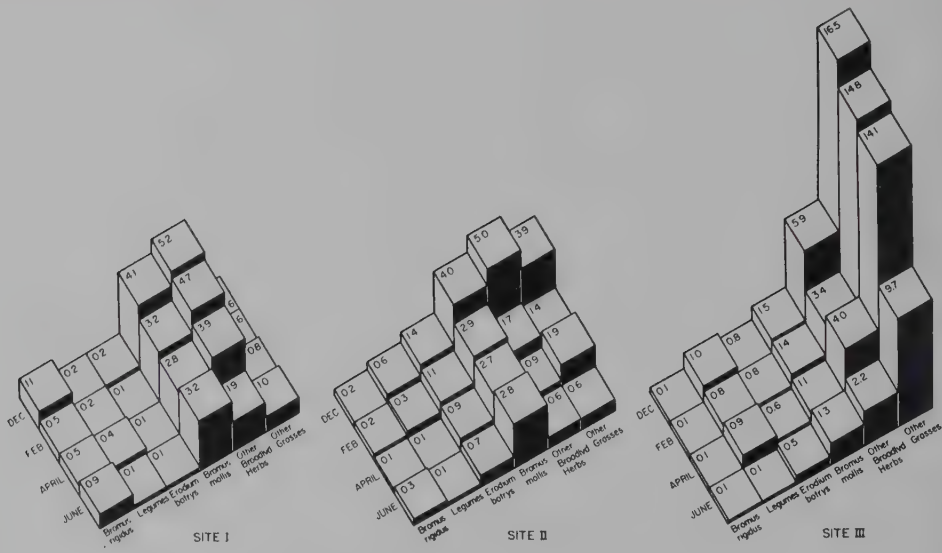
In nearly all cases, there was a reduction in numbers of plants from each sampling date to the next. Two exceptions occurred at Site I and four at Site III (Fig. 6). Thus, in a total of 45 separate comparisons, there were six that showed an increase in numbers from one date to the next. The numbers were equal in two other instances. An analysis of variance showed the reduction between December and June to be significant at the 0.05 level in all cases but 1953-1954 at Site I. The major part of the decrease occurred between December and February and at Site III between April and June. The changes were least between February and April.

CHANGES BY SPECIES FROM DECEMBER TO JUNE

Diverse patterns of change were exhibited by the different species or groups. For two of the sites, much of the seasonal decrease was in the categories of broadleaved herbs and other grasses. Site I showed significant decrease only in the broadleaved herbs. The three species, *Bromus mollis, Bromus rigidus,* and *Erodium botrys,* and the legumes were fewer in number in June than in December, but the differences were not significant (Fig. 7).

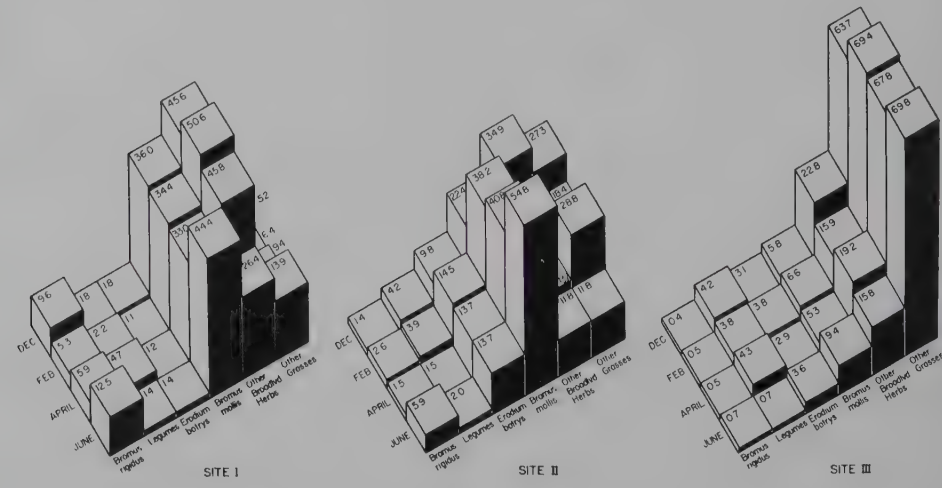
The relative responses by the different species and groups are shown by percentage botanical composition (Fig. 8). *Bromus mollis* and *Bromus rigidus* made up more of the vegetation in June than in December at all three sites. *Erodium botrys* was about the same proportion at all four times of sampling. The legumes generally comprised the least in June and the most in April, although not significantly so and not without exception. At Site I the other grasses increased in importance through the season and at Site II they were irregular. Where they comprised a high proportion of the vegetation (Site III), they held through the season with little change. Other broadleaved plants were irregular but in a decreasing trend.

The percentage botanical composition for *Bromus mollis* and *Erodium botrys* at Site II illustrates change on a year by year basis (Fig.



AVERAGE NUMBER OF PLANTS PER SQUARE INCH

FIG. 7. Average number of plants per square inch for three species and three groups of species at each of four seasons over a period of five years.

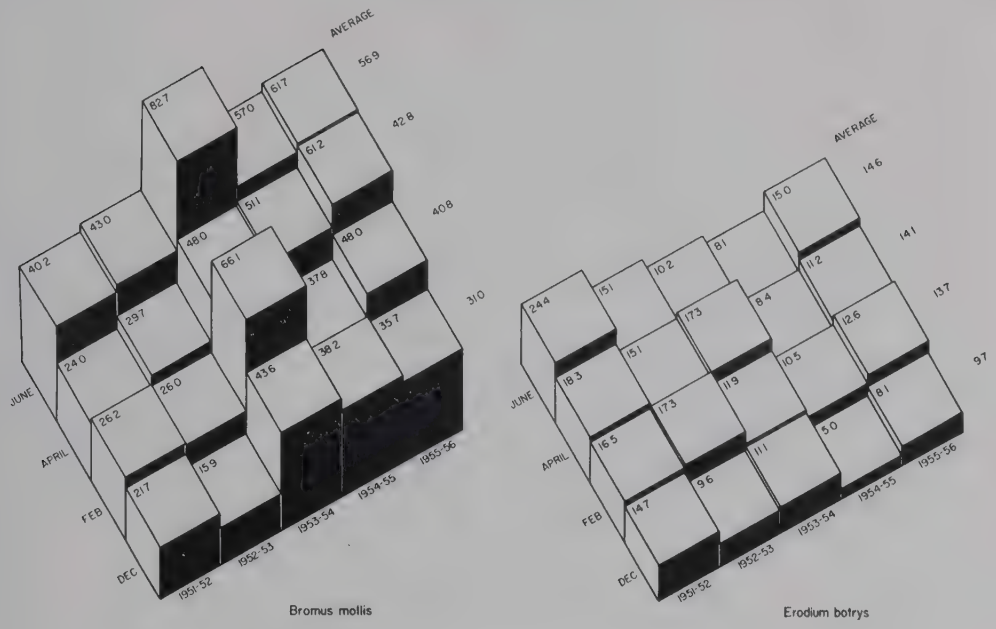


AVERAGE PERCENTAGE OF TOTAL NUMBERS

FIG. 8. Percentage botanical composition for the average numbers of plants per square inch shown in Figure 7.

9). (Note the reverse order of months in this Figure.) For *Bromus mollis* two of the April readings were lower than those from February and one February reading was lower than that in December. The differences in percentages between December and June are significant at the 0.01 level. Somewhat more irregularity existed with *Erodium botrys*. In three of the five years (1952, 1953, and 1956) this species made up more of the vegetation in June than in the previous December at the 0.05 level of significance.

From these data, it would seem that the species



PERCENTAGE OF TOTAL NUMBERS AT SITE II

FIG. 9. Percentage of the botanical composition contributed by *Bromus mollis* and *Erodium botrys* at Site II at four seasons for five years.

with individuals that are relatively small in stature and usually most numerous were the ones that exhibited the widest change in numbers. Even though all species showed mortality as the season progressed, the larger plants, or at least *Bromus mollis, Bromus rigidus,* and *Erodium botrys,* survived better than did the smaller ones. The decrease took place over and above a highly significant difference between years in their relative position.

The pattern of change through each growing season was essentially the same whether density was high or low in December. From this fact it would seem that the relative proportion of plants by species for the entire growing season was established before December of each year. This may in part be due to differences in the amount of viable seed produced the previous year, depredations on the seed during the summer, and climatic conditions previous to and during the first days of the growing season. The relative importance of these factors and others can only be speculated upon at this point.

CHANGES FROM YEAR TO YEAR

The changes from one year to the next are perhaps the most striking of the differences mentioned so far. These have been shown in Figures 6 and 9 and are further illustrated by the numbers in June of each year (Fig. 10). The greatest numbers of plants per square inch at all four dates occurred in 1952-1953 (Fig. 6). This was without exception on the three study areas and was significant at the 0.05 level. The lowest numbers at Site I were in 1955 and in 1952 at the other sites. For the most part the same relative position was maintained through the seasons of each year.

The large numbers in 1953 were made up mostly of *Bromus mollis,* small grasses, and broad-leaved plants. However, the general appearance on all three sites suggested predominance by either *Bromus mollis* or *Bromus rigidus* because they grew luxuriantly that year. The years 1952, 1954, and 1956 were also years of good grass growth but not so much so as 1953 (Figs. 11-12). In these years of moderate grass the vegetation showed much more of a mixture of species in the aspect than in 1953 and 1955.

The vegetation was short and dominated by *Erodium botrys* in 1955 except at Site I even though the plants were few in number that year. The two extreme years for growth and appearance of the vegetation were 1953 and 1955. The vegetation in the former was clearly dominated by

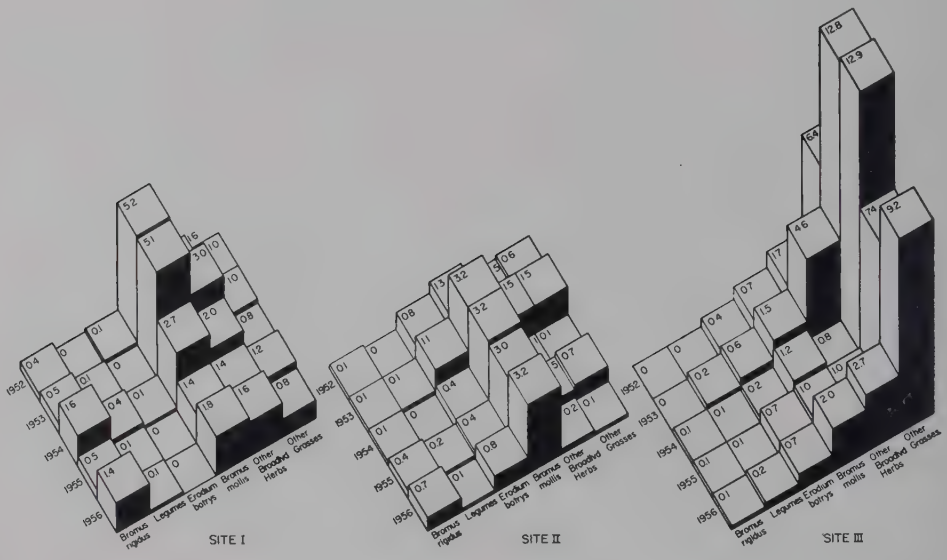


FIG. 10. Average number of plants per square inch in June for three species and three groups of species in each of five years.

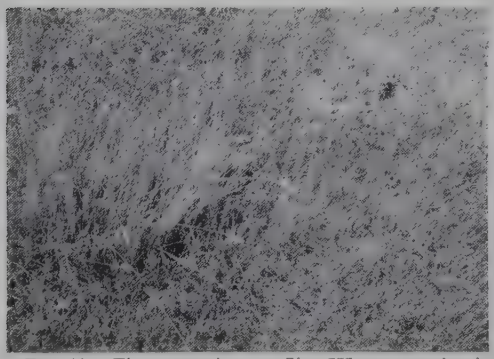


FIG. 11. The vegetation on Site III at maturity in 1952 (see Fig. 12).

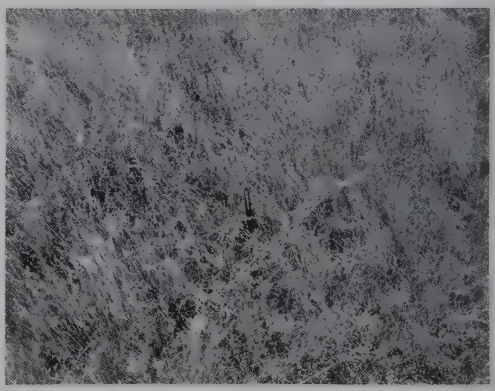


FIG. 12. Same area as Fig. 11 but at plant maturity, 1954. The small grasses were about twice as numerous as in 1952. *Erodium botrys* was most numerous in 1952. In both years *Bromus mollis*, the few tall stems in the photos, was inconspicuous.

grasses and the latter was definitely a year favorable for *Erodium*.

DIFFERENCES BETWEEN SITES

Increasing numbers of plants per square inch were found on Sites I, II and III in that order. Changes in the vegetation betwen seasons and between years were more uniform on Site I than the others. The nature of these changes has been discussed. In this section the consistent differences between the sites over the five years will be discussed.

The sites were characterized in all five years by high proportions of certain species (Fig. 8). Site I had more *Bromus rigidus* than the other areas even though there was less than one per square inch on the average (Figs. 5 and 7). However, it was enough to give the area the general appearance of a stand of *Bromus rigidus* because the plants of this species were taller than the other grasses and broadleaved plants. *Erodium botrys* and the small grasses were inconspicuous.

Site III contained a high percentage of small grasses such as *Festuca dertonensis, Aira caryo-*

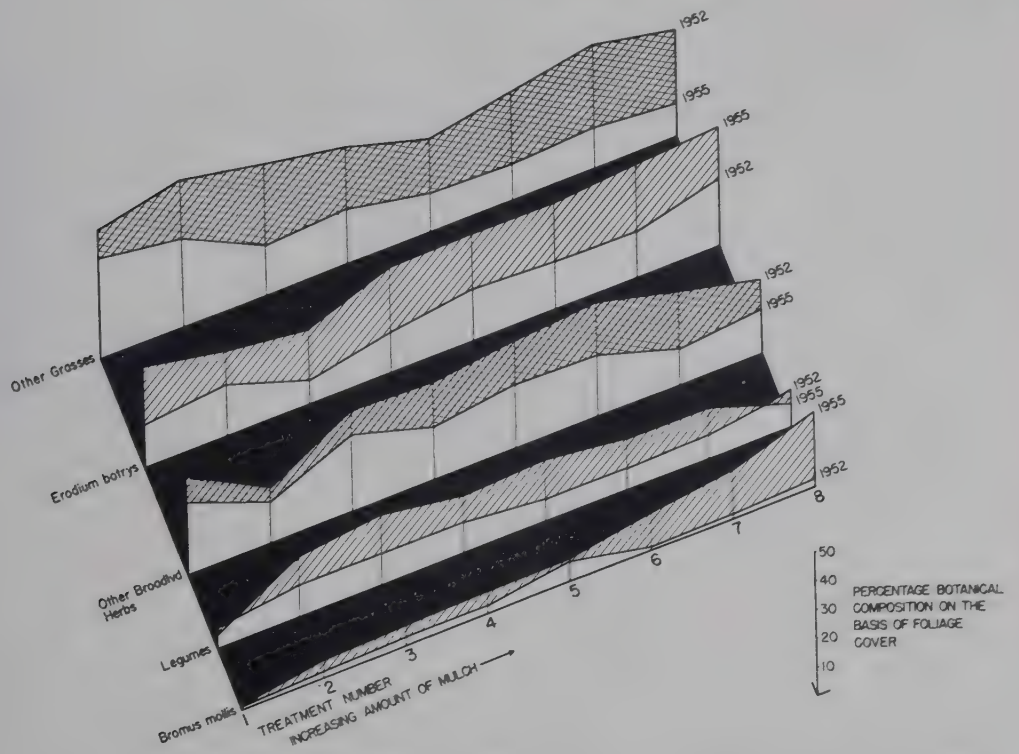


FIG. 13. Percentage botanical composition at plant maturity for two species and three groups of species on a basis of foliage cover. The treatments were amounts of mulch in September of the year preceding and varied from none to approximately 3200 pounds per acre.

phyllea, Briza minor, and *Gastridium ventricosum.* In December and February when the grasses were short, *Erodium botrys* was also conspicuous (Figs. 1-3 and 11-12). Legumes were most numerous at Site III and at times in mid-spring they made a conspicuous show of color.

Site II had the appearance of predominance by *Bromus mollis* even though it was not as numerous as on Site I. This is because *Bromus rigidus* was scarce at Site II. *Erodium botrys* and *Medicago hispida* were also a conspicuous part of the vegetation (Fig. 4). On this site, those species in the categories of other broadleaved plants and other grasses were never very conspicuous even though they were numerous in December. *Daucus pusillus* was another major species here.

CHANGES DUE TO TREATMENT

Vegetational changes in the California annual type have been related to several kinds of treatments (Biswell 1956). Talbot, Biswell, and Hormay (1939) and Bentley and Talbot (1951) described vegetational changes on the San Joaquin Range that were associated with rodent activities and the intensity of grazing by cattle. Jones and Love (1945) described a grazing system whereby early heavy grazing and late deferment were observed to result in a higher proportion of taller grasses and a lower proportion of the early maturing small weeds and grasses. Fertilization has been reported to result in higher proportions of legumes if with phosphorous and more grass if with nitrogen in the presence of sufficient phosphorus (Martin and Berry 1956, Williams, Love, and Conrad 1956). Sulphur fertilization has increased the amount of legumes for a year or so (Conrad 1951, Arkly, Helphinstine, and Williams 1955) and then an increase of grass (Bentley and Green 1954). Burning has also been found to be a treatment effecting changes in species composition. Hervey (1949) reported an increase in weedy vegetation following a grass fire on annual range but if weeds were already dominant litle change was observed. These shifts in composition were probably the result of variations in the amount and position of mulch. The influence of mulch on annual vegetation has been described for the San Joaquin Experimental

Range (Talbot and Biswell 1942) and for the Hopland Field Station (Heady 1956). Some of the data in the latter publication will illustrate the important points (Fig. 13).

In reading the chart, the height of the vertical lines gives the relative importance of each species. The shaded portion shows the difference in percentage composition between the two years. The convergence, crossing, and divergence of the two lines for each year and their position above the base line show the effect of mulch on percentage composition.

Bromus mollis increased in percentage composition with an increase in the amount of mulch. The legumes were low with both extreme amounts of mulch. *Erodium botrys* was not materially affected by the amounts of mulch. *Orthocarpus erianthus, Hypochoeris glabra,* and *Baeria chrysostoma* were conspicuous on the plots with no mulch. In both years shown in the diagram the small grasss were present in large numbers on all plots. They were less abundant with large amounts of mulch.

Figure 13 also shows that the vegetation was different in botanical composition between the two years, regardless of treatment. The small grasses and weeds were sparse in 1955. 1952 was a poor year for legumes and *Erodium botrys. Bromus mollis* was not materially different in the two years. The effects of the mulch treatments can be evaluated only in relation to the yearly differences for all species.

Relation of Weather to Seed Germination

The data presented indicate that many seeds had germinated by December in all years and locations. However, ungerminated seed was seen at that time and some of the seedlings had not developed true leaves. In December of 1954 there were two age classes of the large species such as *Erodium botrys, Bromus rigidus,* and *Bromus mollis.* One crop had survived germination in late August and the other had started in November. In December of 1955 seedlings of the *Trifolium* species were found from the cotyledon to the three-leaved stage and much *Bromus mollis* had recently germinated. An occasional new plant of some of the broadleaved species was observed in February of 1952, 1954 and 1955. Otherwise no germination was observed through the late winter and spring months. Ungerminated seed of *Medicago hispida* was present at all times at Site II (Fig. 14). Not all germination occurred at the same time each year nor was it normally spread over as long a period as in 1954. There seems to be little germination after the first of each year or even after December 1. Well distributed late rains fell in May and June of 1953.

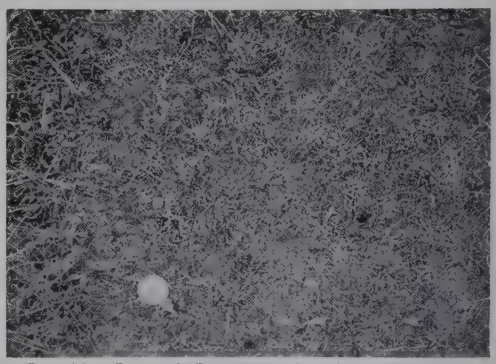


Fig. 14. Seed of *Bromus mollis,* burs of *Medicago hispida,* and heads of *Gastridium ventricosum* on the soil surface at Site II, July 15, 1953.

Plants of *Bromus mollis* continued to develop new culms throughout the spring and seed from the earliest ones had shattered by June. A few of these germinated immediately but none were observed to develop to flowering.

If the numbers of plants in December are taken to indicate favorable or unfavorable conditions for germination and establishment up to that time, it should be possible to correlate plant numbers with climatic conditions. November mean minimum temperatures were about 5 degrees less in 1955 than in the other years and about 5 degrees higher in 1953 (Table I). The total number of plants per square inch was neither lowest nor highest in those years (Fig. 6). Mean maximum temperatures were not greatly different for the Novembers of the 5 years.

On the other hand the greatest number of plants on all sites in December occurred in 1952. That is the year of least rainfall previous to that date and also a year when sufficient moisture to start the plants was late in arriving (Fig. 15). Temperatures were about average during the last two weeks of November of 1952.

The time between sufficient rain for germination and the December sampling in 1953 was the shortest period in five years. Temperatures were warm. *Bromus rigidus* had reached a height of six inches and was stooling, and there were large numbers of all grasses. Many seeds of *Medicago hispida* had germinated but a high proportion of the seedlings were dead because the soil surface was dry before they could become established.

Relation of Weather to Seedling Survival

The total rainfall at headquarters of the Hopland Field Station ranged between 24.8 and 50.9

TABLE I. Temperatures on the Hopland Field Station

	Mean Minimum Temperature				Number of Days with Temp. 31°F and below				Minimum Temperature			
	1952-53	1953-54	1954-55	1955-56	1952-53	1953-54	1954-55	1955-56	1952-53	1953-54	1954-55	1955-56
July		48.7	49.2	44.4		0	0	0		41	42	37
Aug.		47.6	46.8	43.5		0	0	0		42	41	37
Sept.		48.0	42.2	40.9		0	0	0		35	35	32
Oct.		39.5	36.9	36.1		0	8	2		32	27	27
Nov.	36.7	42.0	35.8	30.9	5	2	5	19	27	30	24	24
Dec.	39.8	35.5	29.0	32.0	0	11	23	15	32	25	17	19
Jan.	41.0	33.6	25.5	31.5	2	14	28	14	29	25	19	18
Feb.	35.1	34.4	27.1	24.0	10	8	22	27	29	29	20	16
Mar.	36.3	35.7	28.9	27.2	6	8	21	25	24	27	21	18
Apr.	40.3	41.7	31.8	32.3	3	1	15	9	29	30	24	25
May	41.1	42.1	39.5	36.7	0	1	0	6	35	30	33	31
June	45.1	46.1	42.8	41.9	0	0	0	0	40	36	33	33
		Total			26	45	122	117				
		Date of first frost				Nov. 18	Oct. 24	Oct. 6				
		Date of last frost			Apr. 9	May 1	Apr. 20	May 14				
	Mean Maximum Temperature				Maximum Temperature							
July		93.9	92.3	86.8		103	104	100				
Aug.		84.5	83.4	94.2		100	100	102				
Sept.		88.4	83.5	89.6		107	100	111				
Oct.		76.1	75.3	77.8		94	92	91				
Nov.	63.8	61.3	63.1	61.2	75	81	75	83				
Dec.	52.7	56.7	52.0	53.8	61	67	58	63				
Jan.	56.8	52.3	51.2	50.8	65	61	62	55				
Feb.	62.3	64.2	58.5	55.4	73	80	68	68				
Mar.	61.8	58.8	64.0	63.7	79	76	83	76				
Apr.	68.4	71.0	60.6	66.6	89	92	75	83				
May	69.9	77.9	75.3	74.2	86	92	94	91				
June	78.4	79.8	81.3	83.4	96	105	99	106				

inches for the five growing seasons beginning July 1, 1951 (Fig. 15). The first shower was recorded on July 19 and the last on June 29. However, the effective growing season is much shorter than that. Germination ordinarily begins with the first rain of one-half to one inch and growth ends with dry soil in May or June. The range in date for the first rain of one-half inch or more was eleven weeks, from August 25 to November 13. There was a long dry period after the August 25 rain, until October 7 when 0.5 inch fell and the next was November 8-17 when 5.8 inches occurred. During the five years the range in date of the beginning of continuous wet soil was October 1 to November 13 (Table II). This is the range in time when the hills became green.

In 4 of the 5 years the last effective rain for growth of plants was between April 17 and May 8. These rains varied between 0.8 and 3.9 inches. In 1953 growth was exceptionally good because the soil was wet until June. That year the grasses and certain other species matured before the soil was dry and there were many species of summer growing annuals that were conspicuous. Many species were found in 1953 that were not seen in 1952.

The luxuriousness of the vegetation seemed to be related to the pattern of rainfall, length of dry periods and temperatures after a mid-winter date of approximately January 20. The rainfall ranged between 1.6 and 5.6 inches after a date of March 5. This is approximately the date when temperatures were high enough to permit accelerated growth. Winter dry periods of over 20 days occurred in 3 of the 5 years. There were 48 days in 1953, 38 days and a second period of 47 days in 1955 and 22 days in 1956. Four of the years had a wet period between February 20 and March 20 but it did not occur in the other year until April 16 to 30. In that year it was the last rain of the season.

Three years were very different in these patterns. One, 1953, was the warmest winter and had scattered spring rains of sufficient amount to allow the vegetation to develop even though there were 48 days of dry weather between January 21 and March 19. Numbers of plants were highest throughout that year. In 1955 there were 86 days between January 21 and April 16 with only 2.9 inches of rain and the winter was relatively cold. This was followed by 3.9 inches in late April which was sufficient to permit fair forage production of some species but *Festuca dertonensis*, for example, was mature and did not respond.

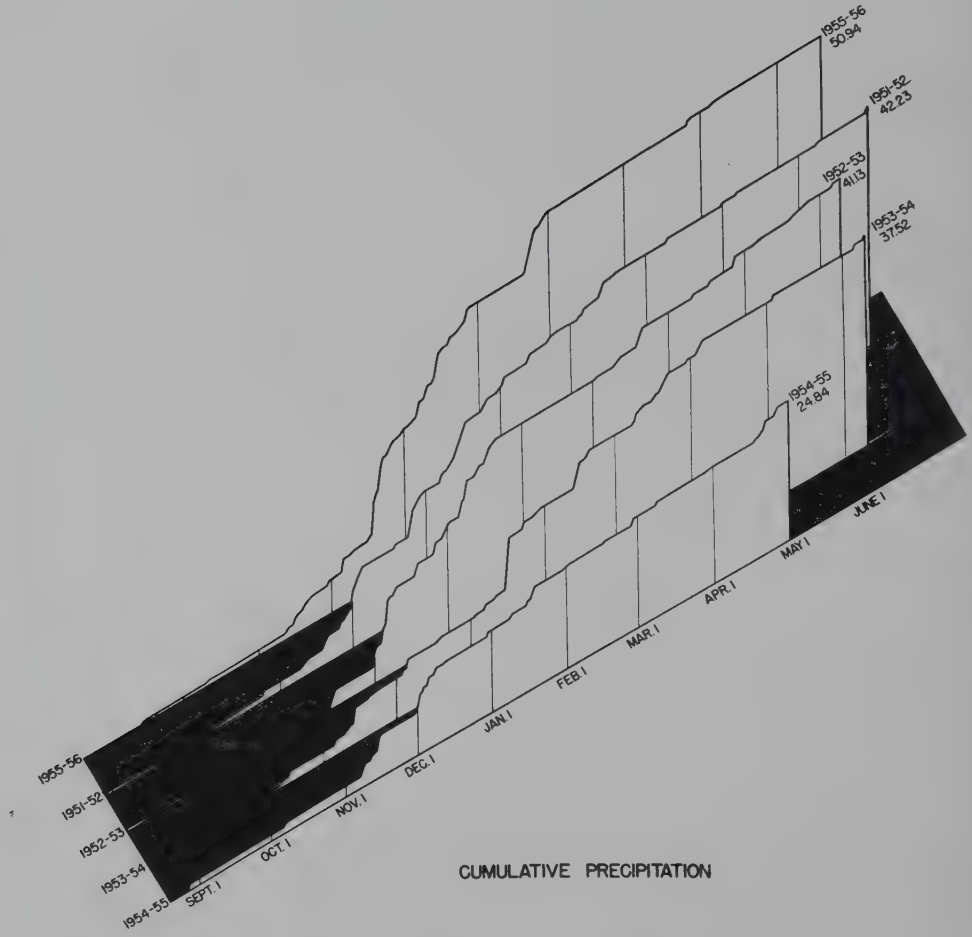


FIG. 15. Cumulative precipitation on the Hopland Field Station during each of five growing seasons. Horizontal portions of the graph indicate periods without precipitation.

The number of plants per square inch was low during that year. In 1956 the total precipitation for the season was high but there was only 1.62 inches after March 5. That spring was a cold one. The grasses did not do well, but *Erodium botrys,* on the other hand, made excellent growth.

In the fall of 1954, *Medicago hispida, Erodium botrys,* and *Bromus mollis* germinated after August rains. Many plants of the latter two species lived through the ensuing drought but those of *Medicago* did not.

In two of the years, 1952 and 1954, there was over one inch of rain in June. In neither of these years were the summer growing plants obviously more abundant than in years of no late rain.

On numerous occasions during the December and February samplings, frost heaving of the soil was observed where mulch or moss was scarce. Some plants were actually lifted from the soil. The most severe damage occurred at Site II where frost heaving resulted in small areas of bare soil. Plants of all species except *Bromus mollis* and *Erodium botrys* were susceptible. Frost heaving may explain the pattern of botanical composition at Site II.

Heaving of plants from the soil by frost was not observed in Site I and only in slight amounts in February of 1952 and 1954 at Site III. There was always a protective layer of mulch or moss on these areas during the winter and they were less subject to cold air drainage than Site II.

Frost or freezing did occur at all the sites as

TABLE II. Patterns of precipitation on the Hopland Field Station

Season	1st rain of ½" or more		Second rain if 1st less than 1 inch		Last effective rain for growth		Winter dry periods over 20 days		Rain after T. begins to rise		Rain after veg. dries	
	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.	Date	Amt.
1951-52	Oct. 1	0.50	Oct. 24	1.00	Apr. 30 May 8	0.85	None Jan. 21-	0.43	Mar. 19	2.80	June 6-29	1.53
1952-53	Nov. 12-16	2.74			June 6-10	0.85	Mar. 9 48 days		Mar. 29	5.64	None	
1953-54	Oct. 14-19	1.46			May 3	0.75	None		Apr. 5	2.12	June 5-9	1.07
1954-55	Aug. 25-29	1.07	Oct. 7-8	0.50	Apr. 17-30	3.86	Jan. 21- Feb. 26 38 days	0.69	Jan. 20	6.96	None	
			Nov. 8-17	5.84			Mar. 1- Apr. 16 47 days	0.60	Apr. 30	None		
1955-56	Nov. 13-24	4.22			Apr. 25-27	0.92	Jan. 28- Feb. 18 22 days	0.02	Mar. 5	1.62	June 19	0.09

evidenced by damaged leaves of the grasses. Frost injury of range annuals has been examined by Laude and Berry (1957). Although frost heaving has been observed to result in seedling mortality, it cannot be considered the sole cause in the death of plants because the decrease in number occurred where frosts were light as well as where they were heavy.

Relation of Grazing to Changes in Seedling Numbers

Both sites II and III were in a pasture grazed by sheep (Fig. 16). Site III was closely grazed and heavily trampled because it was located close to a feeding place. Grazing was estimated to be close in December of 1951; February of 1952, 1953, and 1956; and April of 1954 and 1955.

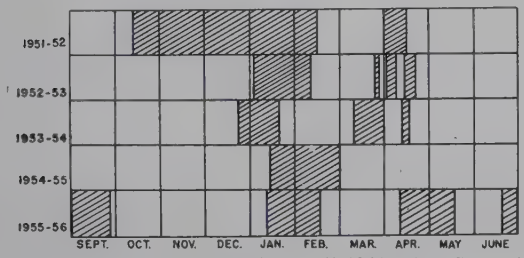


FIG. 16. Periods of grazing, 1951-1956, when Sites II and III were used by sheep.

Site II was located about one half mile from where the animals were fed. This site was grazed frequently and was recorded as closely grazed in December of 1951, and February of 1952 and 1956. In June of 1956 use was selective on patches of *Bromus mollis* and *Medicago hispida*. Usually the grazing was moderate at Site II. The intensity of grazing was indicated by the number of sheep pellet groups on an area of 40 by 40 feet (Table III).

TABLE III. Number of sheep pellet groups on an area 40 by 40 feet

	February		April	
	Site II	Site III	Site II	Site III
1953	37	65	13	92
1954			92	152
1955	19	44		
1956	21	75		

One might expect that grazing would be on the tallest plants first and that this would result in fewer tall plants and more of the short ones. Since *Bromus mollis* and *Bromus rigidus* were the tallest plants immediately after germination as well as at maturity, it would be logical to assume that they would be grazed most intensively throughout the growing season. Removal of the uppermost node stops growth of that culm but does not kill the plant. Additional growth is gained by the proliferation of new culms (Laude 1957). Both tall species showed an increase in proportion of total numbers as the season progressed and all species decreased in numbers with or without grazing. Therefore, changes in the numbers of plants per unit of area could not be related to differential grazing.

Deer on the Hopland Field Station graze the green herbaceous plants during the winter months. They no doubt used all three sites but only on Site I was their use evident in grazed plants and trails across the plots. This is a small area of grassland adjacent to a large timbered area and therefore deer were attracted to it. Only once was deer use recorded for April. Generally their diet

switches to other forages in early spring. By plant maturity all evidence of grazing on herbaceous plants was eliminated.

Rodents, mainly mice, were common at Site I and their activities were always conspicuous. There were no signs of mouse activity at the other two sites. A colony of ground squirrels made numerous trails through the vegetation at Site II. The influence of these animals upon the changes in composition was estimated to be slight.

Relation of Mulch to Changes in Seedling Numbers

The change in general appearance at Site I through the growing season was from large amounts of standing dry plant materials in December to patchy dry and green plants in midwinter and finally to an even stand of tall grass at plant maturity. Usually there was a heavy matted mulch on the soil surface for most of the winter. The mat tended to disappear in late spring but in 1956 little was present after February.

At Site II, mulch was always less in amount and more patchy in appearance than that on Site I. The trampling and grazing of both sheep and deer removed the mulch or matted it on the soil where decomposition proceeded at a fast rate.

Site III was still more heavily grazed and trampled than Site II and consequently, less mulch was present there. The mulch was ordinarily patchy in December and varied from none in 1951 to a nearly complete cover in 1954. Essentially all was gone by June of every year.

The changes associated with amounts of mulch illustrate progressive changes in the annual type. Grazing and fire destroy the mulch; as a result certain species increase. With large amounts of mulch other species are abundant. With no grazing or fire to remove the mulch, *Bromus mollis* and *Bromus rigidus* become the major species in the annual grass type in this location. Others do not replace them and therefore they may be considered the highest species successionally among the annuals.

The amount of mulch greatly influences the speed of early fall growth. Three weeks after the first fall rains *Bromus mollis* was found to be about 2 inches taller on the areas with the most mulch than where there was none. Thus, conditions favor this species at the time of earliest growth because the other species do not respond as quickly. The result is that herbage in grams per square foot was found to be about two and one-half times greater with all the mulch than where there was none.

Discussion

All the changes given in this paper are included under the title of "vegetational changes." Five levels of change have been discussed by Major (1951) as seasonal, annual, successional, historical, and genetical. The data from the square-inch plots illustrate the first two types; the data from the study involving manipulation of mulch illustrate the third or successional change.

Seasonal and annual changes are of the nature of fluctuations in that no evidence of a constant direction toward the dominance or disappearance of one or more species was found. The fluctuation suggests a response by each species population to the incoming heat, moisture, and light as modified by the vegetation itself. The magnitude of these incoming factors varies from season to season and year to year, as does the vegetation. The implied relationships are mentioned because they are usually given as the cause of changes in the California annual type. However, no correlations that suggest cause and effect, except the most general, could be found among the vegetational changes on the three sites. This may be because the only weather data available was of the usual type collected by a standard station about one mile distant. Data on the microclimate might well have shown clearcut relationships between vegetational changes and the micro-environment.

The data from the study on the vegetational changes that were associated with manipulating mulch are presented to illustrate directional changes. These are plant succession. Actually, the data document only one way by which man can influence vegetation of the type studied.

Ecologists have usually studied succession by comparing the vegetation in different areas to arrive at successional stages or sequences by deductive reasoning. But succession is a natural change over time on *one* area. The changes are directional; eventually they may lead to a stabilized vegetation, and they exhibit the oscillations mentioned above. Exclusively inferential conclusions are to be avoided whenever possible because they may be in error as generalities and because they do not allow prediction with accuracy of the details in the successional pattern. Quantitative data are needed on the vegetation of one area over time and should be taken in such a way that the non-directional fluctuations are also measured and separated from successional changes. The separation may or may not be important. In the California annual type, yearly fluctuations are as contrasting as successional stages in many other vegetational types.

Ordinarily it takes years of continued sampling

to gather data on succession, consequently deductive methods are often used. One approach to shorten the time scale is to vary a factor experimentally in such a way that the resulting treatments approximate those that occur over a longer time scale. This was attempted by manipulating the natural mulch. The associated vegetational differences that developed with all mulch removed, none removed, and some intermediate treatments might well indicate the succession of plants in response to natural accumulation of organic material.

The hypothesis was that varying amounts of mulch would favor different kinds of plants, which was found to be true. The deduction was made that the changes in botanical composition represent a successional series. Stable vegetation of the California annual type was assumed to require mulch accumulation to a point where annual increment and decomposition reach stability. This point is as yet untested. Stability is interpreted to include seasonal and annual oscillations.

In the mulch study, the seasonal variations in vegetation were by-passed in the sampling procedure by reading the plots at plant maturity each year. The yearly changes are shown. Above these are the successional changes, which have already been discussed. In the following outline a division of the successional changes is proposed.

I. Primary succession. This type begins on new areas at the same time *zero* as the beginning of soil formation.

II. Secondary succession. Here is included those directional changes toward stability which occur after destruction, partial or complete, of existing vegetation. The destruction may be the result of natural catastrophes or man caused. Time limits on the speed of destruction are not implied. Secondary succession can be divided into two categories:

1. Those beginning from a natural catastrophe.

2. Those beginning from a man controlled cause and so named according to the cause; such as fire; grazing, logging, fertilization, and selective kill of certain species by chemicals. In this context nature plays an important role. A different cultivated crop on a certain field each year would not qualify, but the directional change following abandonment of the field from cultivation would qualify.

Ordinarily, secondary succession should be distinguished from primary succession on the basis of correlation with time zero in process of soil formation. In secondary succession, seldom are both soil and vegetation destroyed to the same extent. The balance is unstable and successional changes occur rapidly until they are in more or less stability with the soil. This implies that soil is ordinarily not set back as far as the vegetation.

Summary

1. Changes in the California annual type were studied on three sites during five successive growing seasons, 1951 to 1956. The sites were located on the Hopland Field Station in Mendocino County. The field data were collected by counting the number of plants by species on quadrats of one square inch in size.

2. The three sites were characterized by distinctly different combinations of annual plants throughout the study.

3. The seasonal growth pattern proceeds from germination, usually in November, through a short period of moderate growth, then a longer winter period when growth is slow, and finally ends with about a month of fast growth in April and May.

4. Average number of plants per square inch varied between 3.3 and 35.0 with different situations.

5. All species decreased in numbers per unit of area from December to June.

6. *Bromus mollis, Bromus rigidus,* and *Erodium botrys* decreased less in numbers per unit of area than the others and, thus, increased in percentage botanical composition.

7. The numbers of plants per unit of area varied greatly between years as also did the various species. For example, 1953 was a year when the grasses clearly dominated the vegetation. *Erodium botrys* constituted a larger portion of the vegetation in 1955 than in other years.

8. The patterns of seasonal and yearly change were recorded on the three sites, with different combinations of the botanical composition of the annual species.

9. Changes in the annual-type vegetation due to such items as grazing, seeding, fertilization, and fire are reviewed and the influence of mulch on percentage botanical composition is illustrated.

10. Data and observations indicate that most of the germination occurs in a short period after the first fall rains of 0.5 to 1 inch. Cause for the differences in total numbers of plants between years was not found.

11. The changes were examined in relation to the patterns of rainfall and temperatures and to grazing.

12. The results are discussed as illustrations of seasonal, annual and successional changes in vegetation.

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GROWTH OF NATIVE AND EXOTIC PLANTS UNDER CONTROLLED TEMPERATURES AND IN THE SAN GABRIEL MOUNTAINS CALIFORNIA[1]

Henry Hellmers and William C. Ashby[2]

Introduction

Plant selection is one phase in the development of methods for soil stabilization in the San Gabriel Mountains of California (Sinclair 1954, Horton 1949). The climate—hot, dry, rainless summers and cool, wet winters—excludes many species of plants from the flora of these mountains. The studies reported here served as a rapid preliminary screening process to select exotic species for erosion-control plantings. Of 24 exotics tested, only one appeared outstanding for erosion control. Three leguminous species were well adapted and were considered desirable for their soil-improving possibilities. The study provided an insight into the autecology of the test species.

The main vegetation type in these mountains at elevations from 1,000 to 6,000 feet is known as chaparral, and is primarily composed of evergreen sclerophyllous shrubs. Jepson (1925) describes the species of the chaparral, which he considers a fire type formation in his discussion of the vegetation of California. An important reference chiefly concerned with the chaparral in northern California is Sampson (1944). Horton and Kraebel (1955) give detailed information on the local southern California species, and on the environment with particular reference to the major factor of fire and its consequences. Many of the species have deep and spreading root systems (Hellmers, Horton, Juhren, and O'Keefe 1955).

Various attributes of the climate in southern California, including several classifications in terms of climatic regions, are presented by Visher (1954). In the Köppen classification this area is represented as a *Cs*, Mediterranean, region. Figure 1 presents data for a station at 2,800 feet within the chaparral formation. The dry season often exceeds 6 months' duration, and has maximum air temperatures of 30° to 40°C. During

[1] Report of research carried on cooperatively by the California Forest and Range Experiment Station and the California Institute of Technology. The former is maintained by the Forest Service, U. S. Department of Agriculture, in cooperation with the University of California, Berkeley, California.

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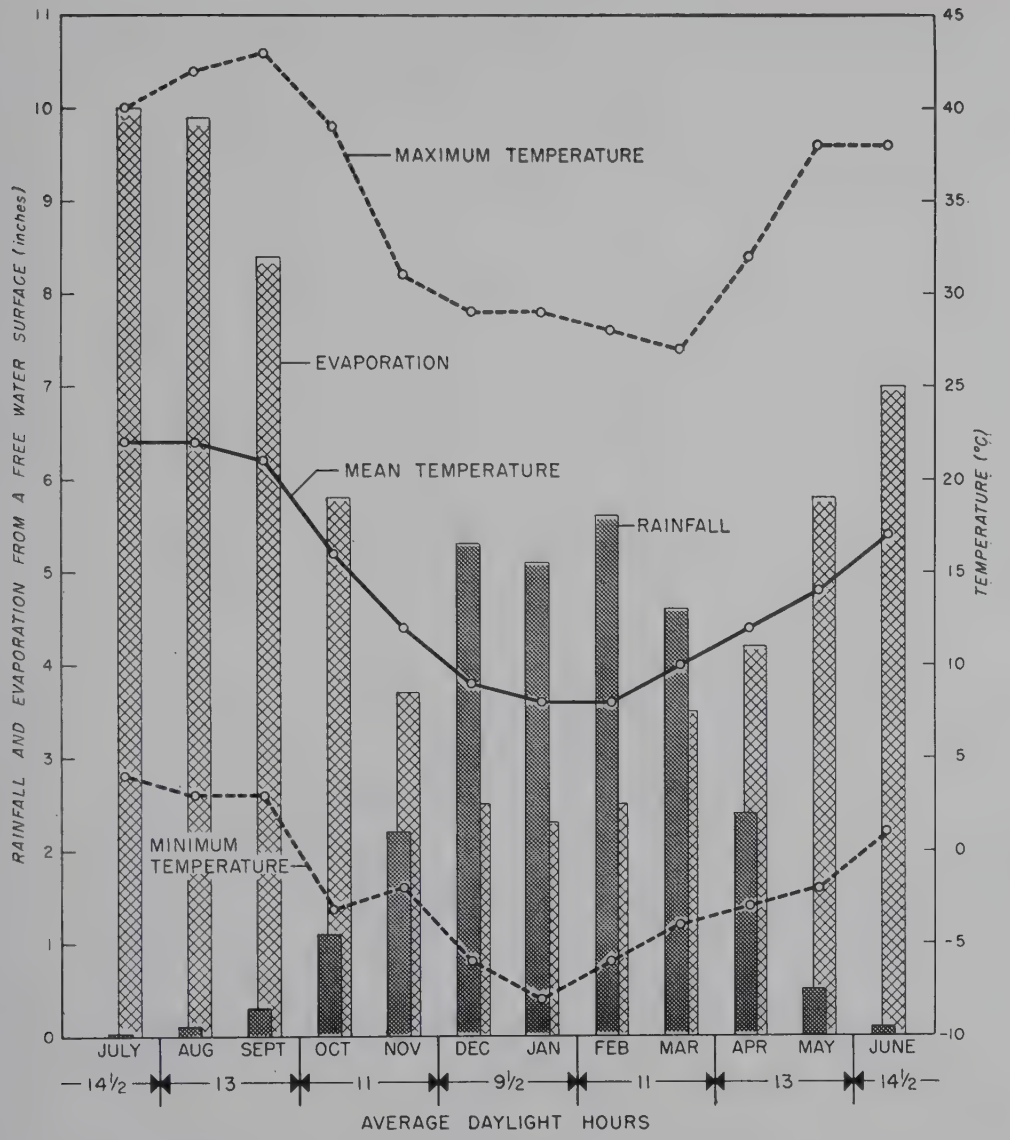
MAXIMUM TEMPERATURE
EVAPORATION
MEAN TEMPERATURE
RAINFALL
MINIMUM TEMPERATURE
RAINFALL AND EVAPORATION FROM A FREE WATER SURFACE (inches)
TEMPERATURE (°C)
JULY AUG SEPT OCT NOV DEC JAN FEB MAR APR MAY JUNE
14½ 13 11 9½ 11 13 14½
AVERAGE DAYLIGHT HOURS

FIG. 1.—Climatic conditions at the 2,800-foot elevation (Tanbark Flat) on south side of the San Gabriel Mountains, California. Average rainfall is for a 27-year period; average pan evaporation, a 20-year period; and air temperature, a 22-year period (Sinclair, Hamilton, and Waite 1953).

the wet winter season, minimum temperatures vary from a few degrees above to a few degrees below freezing. Diurnal variations of 20°C are common in all seasons of the year. About three-fourths of the annual precipitation falls in 4 months, December through March. The average annual rainfall is 20 inches at the base of the mountains (1,000 feet elevation) and increases to 40 inches near the top of the mountain ridge (6,000 feet elevation).

The mountain soils in general are shallow, sandy to rocky, and of low fertility (Hellmers, Bonner, and Kelleher 1955). Only a relatively small amount of the water that falls is retained for plant growth in the soil and the fractured underlying rock after the rainy season (Rowe and Colman 1951).

The limited amount of soil moisture retained past the wet season is rapidly lost through evaporation and transpiration. In late spring, summer,

and early fall, then, lack of soil moisture prevents plant growth. Long ago, Plummer (1911) picturesquely described this relation between plant growth and the seasons, and the strange aspect of the mountains to southern Californians who once lived in regions of summer rainfall:

> "We usually think of springtime as the season when plants begin their growth and when deciduous trees and shrubs spread a new foliage which remains green until autumn. In the chaparral area this is reversed, and the various species make most of their growth during the winter. Through the summer season the mountains are brown, and from a distance look lifeless. Immediately on the advent of winter rains the whole country puts on a vesture of green which remains all winter."

The phenology data reported by Miller (1944, 1947) show that Plummer's observations were at least qualitatively if not quantitatively correct. Most chaparral plants begin growth in early winter but many make their maximum growth in late winter and early spring.

Temperature, through its control of growth processes, may limit the season of plant growth and species distribution. Went (1953) reviewed the subject of temperature effects on plant growth. In the same year Hiesey (1953) published his findings relating growth and development under controlled temperature conditions to the field performance of species and hybrids of *Poa*.

The knowledge of temperature conditions and moisture patterns in the San Gabriel Mountains made possible conducting a laboratory study to screen exotic species for potential erosion control use in these mountains. Plants that grew well in the laboratory under temperatures that occur in the field when soil moisture is available were then field tested for frost hardiness and drought resistance.

Materials and Testing

The choice of exotic plants for testing had to be made as carefully as possible because testing time and greenhouse space were limited. The study was started by surveying various literature references for suggestions and information on plants that might be considered for use in the San Gabriel Mountains (Heacox 1951). The literature search was supplemented by conferring and corresponding with staff members of universities, botanical gardens, city and local nurseries, arboreta, state and federal agencies, and others. Additional information and seeds were obtained through biologists living in other regions of the world with Mediterranean-type climate.

The plants tested had characteristics considered suitable for soil stabilization. They were either prostrate, bushy, or leguminous, to furnish maximum soil cover or to serve in soil improvement. Exceptions were made to include species that exhibited outstanding growth rates in their native habitats.

The selected species were tested in the air-temperature controlled greenhouses and chambers of the Earhart Plant Research Laboratory (Went 1950, 1957). Species native to the San Gabriel Mountains were grown for comparative purposes in the study.

All plants were grown individually in gallon cans with a medium of crushed gravel, and watered with Hoagland's nutrient solution (Hoagland and Arnon 1950). Sunlight in the greenhouses reached 7,000 foot candles in December, and increased to 10,000 foot candles in May (Ulrich 1952). This December light condition is sufficient for good plant growth. As the laboratory is kept free of insects, the plants suffered no deformity due to pests.

The plants were established under temperature conditions of 23°C days and 17°C nights. Plants of most species were grown to the two-leaf stage before placing them under test conditions. Small-seeded species were grown to a larger size, usually the four- to six-leaf stage. For all species the plants were selected for uniformity before being placed under the temperature treatments.

The day and night temperatures used in the study were based on an analysis of the monthly maximum and minimum air temperatures recorded in Weather Bureau type shelters at elevations of 1,500; 2,800; and 4,350 feet on the San Dimas Experimental Forest in the San Gabriel Mountains. Figure 1, for example, gives the absolute maximum and minimum temperatures for the 2,800 foot station. Averages were determined for winter, spring (or fall), and summer day and night temperatures. Temperatures decreased with increasing elevation. The conditions of the 17°C day with 17° night, and the 23°C day with 26° night were included to aid in interpreting the effectiveness of day versus night temperatures on the plant responses.

Growth response to temperature was determined by growing plants of each species under eight different temperature conditions. The separate effects of day and night temperatures were included in the test. Under one series of conditions the day temperature was held constant and different night temperatures were used. Under the other two series, the night temperature in each was held constant while different day temperatures

were used. The temperatures used were 23°C days in conjunction with 4°C, 10°C (spring and fall), 17°C, and 26°C nights. Day temperature effects were obtained by adding the following four conditions: 30°C and 17°C days with both 4°C and 17°C nights. The 17°C day and a 4°C night represented the winter condition, while the 30°C day and the 17°C night represented the summer condition. A day consisted of 8 hours and a night was 16 hours in this study.

The plants were grown under the test conditions for 24 weeks. Duplicate plants were grown under the seasonal temperature conditions as a check against differences within species due to genetic variability. The morphological characteristics of the plants were noted during the 24-week period. When plants were harvested, dry weights of tops and roots were obtained.

The more promising species from the laboratory study were field tested to determine their frost hardiness and drought resistance. Transplants were established on three sites in the San Gabriel Mountains. Two sites, at elevations of 2,700 and 5,100 feet were on ridges. The third site, at 2,800 feet elevation, was on a man-made terrace in a hillside with western exposure. Potted transplants were used. The plants were set out in the spring of two successive years and were watered monthly through the first summer. Watering was stopped in August to allow the plants sufficient time to harden before the winter frosts. The plants were fertilized with nitrogen during the first winter.

Treatment and Performance by Individual Species

Plant growth in the laboratory varied by species and temperature conditions. Some species could not survive the cool winter conditions; others failed under the high summer temperatures. Plants of many species survived and grew under the complete range of temperature conditions.

Dry weights of the different plants grown under the eight temperature conditions are presented in Table I. For the plants at 17°C day, 4° night; 23° day, 10° night; and 30° day, 17° night the values are generally a mean of two replicates. Occasionally replicates were grown at one or more of the other sets of temperatures. The variation between replicates ranged from 0 to 50%, while differences between plants at extreme temperature conditions were often several hundred percent. Treatment procedures and observed growth characteristics of each species tested in the laboratory and field are described in the following paragraphs. Treatments used to stimulate germination were mostly those described by Mirov and Kraebel (1939).

Native or resident species

Adenostoma fasciculatum H & A.—A native dominant shrub (Rosaceae) present in the southern California chaparral. Germination was obtained by giving the seeds a heat treatment before planting. The seeds were mixed with vermiculite, heated to 100°C, and then allowed to cool (Sampson 1944, Stone and Juhren 1953). This species grew under all of the temperature conditions of the test, but was favored by the early spring or late fall temperature conditions of a 23°C day and 4°C or 10°C night. The plants tended to fall over and then send up new lead shoots. Branching was profuse. During the 24-week study period only juvenile type foliage was produced. The dense fibrous root system spread evenly throughout the entire planting medium.

Bromus rigidus Roth.—This grass originally from the Mediterranean is now considered a resident of southern California. It invades openings in the brush where the soil has been disturbed. Seeds of this species germinated quickly without pretreatment. The plants grew similarly under both winter and spring conditions. The plant producing the most tillers, 618, was grown under the 23°C day and 4°C night condition. The high day temperature of 30°C retarded growth, irrespective of the night temperature. Plants grown under a 30°C day had the fewest tillers, 165 per plant. The 30°C day also caused the plants to have narrow leaves. The fibrous root system formed a dense mat throughout the gravel medium.

Ceanothus crassifolius Torr.—A non-sprouting shrub (Rhamnaceae) dominant in southern California chaparral after fires. The seeds required soaking in hot water overnight, followed by one month of stratification at 4°C before planting. Growth of these plants was restricted by cold nights (4°C). All of the plants grew erect. The roots were white, thick, and brittle except those grown under the 23°C day and 26°C night which were gray and fine. The roots were concentrated in the bottom of the container.

Melica imperfecta Trin.—A native bunch grass found in association with the chaparral. The seeds required no pretreatment, but germinated best under moderate temperatures (Ashby and Hellmers 1955). Day temperatures had relatively little effect on tillering. The number of tillers, however, varied with the night temperatures. More than 300 tillers per plant were produced under night temperatures of 10°C and 17°C, while less than 200 tillers were produced under night temperatures of 4°C and 26°C. All plants grown at the 17°C and the 10°C night temperatures flowered.

TABLE I. Twenty-four weeks growth, in grams of dry weight, of native and exotic shrubs under eight sets of controlled temperatures. Day temperatures (D) were for 8 hours, and night temperatures (N) were for 16 hours in each 24-hour period

Species	Temperature Conditions															
	17°C (D) 4°C (N)		17°C (D) 17°C (N)		23°C (D) 4°C (N)		23°C (D) 10°C (N)		23°C (D) 17°C (N)		23°C (D) 26°C (N)		30°C (D) 4°C (N)		30°C (D) 17°C (N)	
	Top	Root	Top	Root	Top	Root	Top	Root	Top	Root	Top	Root	Top	Root	Top	Root
Natives and Residents:																
Adenostoma fasciculatum	4.7	0.8	...	...	11.5	2.4	12.4	2.0	7.5	1.2	0.8	0.1	3.2	0.4	4.0	.50
Bromus rigidus	49.2	8.6	33.9	8.2	55.2	8.8	58.0	10.8	43.3	6.4	31.4	4.0	22.2	4.3	25.0	6.1
Ceanothus crassifolius	4.1	1.4	10.2	2.3	....	....	8.9	2.0	7.9	1.7	5.6	1.0	4.4	1.1	5.8	1.3
Melica imperfecta	13.7	2.8	51.2	5.4	16.2	3.0	54.9	3.4	52.6	3.7	5.2	0.5	2.7	0.5	33.8	3.2
Quercus dumosa	1.2	1.4	2.5	2.4	0.9	1.2	1.3	2.0	0.9	0.8	3.7	2.5	0.6	1.0	5.0	2.8
Rhus laurina	1.6	0.2	13.5	4.3	5.7	0.6	14.7	2.9	19.6	6.4	26.0	6.2	7.4	1.4	49.8	9.5
Rhus ovata	0.1	0.1	2.8	0.7	0.8	0.6	3.0	1.9	1.6	1.0	9.6	3.4	*	*	4.4	2.0
Salvia mellifera	2.2	1.2	1.2	†0.6	8.8	3.0	6.9	3.6	12.4	4.8	*	*	4.2	1.2	8.3	1.7
Exotics:																
Baccharis pilularis ssp. *typica*	15.5	3.7	29.5	6.6	33.1	10.0	24.1	4.2	16.6	3.7	17.9	5.4	8.6	2.3	23.8	4.4
*Brassica nigra***	7.7	2.0	15.9	5.6	14.9	3.6	24.1	6.7	28.1	5.5	17.1	3.8	6.0	0.9	15.8	2.2
Bromus stamineus	47.0	14.8	49.7	12.6	51.1	13.5	69.6	15.0	70.0	14.4	21.2	5.2	14.0	5.7	35.2	7.1
Buddleia globosa††	3.1	2.0	15.4	4.2	3.8	1.8	2.8	1.1	22.4	4.2	16.8	4.5	5.2	2.4	13.0	2.8
Calycotome villosa	3.2	1.5	4.6	1.8	0.9	0.5	20.4	4.0	13.3	2.8	19.7	6.0	3.8	1.4	24.6	4.6
Cassia acuta	*	*	14.3	3.6	4.5	2.4	24.3	5.7	32.4	7.8	22.9	2.2	11.7	3.2	39.6	7.3
Cneoridium dumosum	*	*	3.4	1.3	0.4	0.2	3.0	0.8	6.5	2.1	1.8	0.5	0.4	0.1	1.6	0.4
Convolvulus althaeoides	1.3	0.7	0.5	†0.3	5.1	4.3	2.3	1.2	4.7	1.9	1.7	0.9	*	*	*	*
Cytisus canariensis	10.5	2.9	28.3	8.3	9.2	3.8	80.8	17.2	45.3	13.6	62.6	13.9	7.5	3.2	22.5	6.5
Dodonaea viscosa var. *angustifolia*	0.2	0.2	8.0	1.6	3.1	1.1	5.9	1.8	18.2	2.6	41.6	6.2	3.4	1.0	41.4	6.8
Ehrharta calycina	21.8	3.6	34.6	3.7	57.4	7.2	47.8	4.7	58.6	4.3	14.7	1.1	18.6	3.4	28.8	3.9
Forestiera neomexicana	*	*	0.1	0.1	0.1	0.1	0.1	0.3	1.8	1.6	....	....	0.2	0.2	3.0	1.0
Lolium multiflorum	69.2	9.4	107.5	7.0	62.1	4.0	70.9	7.0	58.6	4.1	....	....	29.4	4.3	53.4	4.2
Lotus bertholetii	15.4	1.8	23.6	3.3	26.0	1.7	11.6	1.0	9.5	0.7	7.7	0.4	4.4	0.2	2.9	0.2
Lotus mascaensis	14.9	3.6	21.4	3.4	11.6	1.5	32.2	4.2	11.8	1.4	....	....	30.2	2.4	32.2	2.8
Lygeum spartum	0.9	0.3	3.5	0.8	1.3	0.2	4.8	1.0	4.6	0.8	5.1	0.8	1.4	0.2	3.6	0.6
Phalaris tuberosa var. *stenoptera*	36.8	10.2	32.0	6.6	39.4	9.4	48.8	13.6	36.3	6.9	25.3	7.2	19.2	6.5	23.5	4.4
Pinus brutia	1.0	0.8	2.5	1.2	0.7	0.7	1.9	1.2	2.6	1.6	2.7	1.2	1.3	0.6	2.9	1.1
Retama raetam	2.0	0.6	2.3	0.5	1.2	0.4	2.1	0.6	2.4	0.6	1.4	0.2	0.6	0.2	2.0	0.4
Schinus dependens	0.8	0.6	5.7	1.8	4.9	2.0	18.1	4.4	22.1	4.2	18.2	4.4	5.2	1.7	23.8	6.4
Sophora tetraptera	0.3	0.2	7.6	2.6	0.5	0.3	3.5	1.6	7.1	2.8	3.2	1.2	0.2	0.1	2.9	1.2
Spartium junceum	1.3	1.0	14.3	5.5	3.3	1.8	11.7	3.4	15.4	4.2	13.4	2.2	4.2	1.9	29.6	6.4
Zizyphus lotus	*	*	0.1	0.1	0.4	0.2	0.4	0.1	0.5	0.7	10.8	4.2	0.4	0.2	3.9	3.8
Zizyphus nummularia	*	*	0.2	†0.3	0.3	0.2	1.9	0.4	2.9	3.3	1.2	0.7	1.0	0.6	1.2	0.6

*Died. †10°C night temperature in place of 17°C. **Harvested after 10 weeks. ††Harvested after 8 weeks.

Quercus dumosa Nutt.—This is the scrub oak (Fagaceae) of the chaparral. The acorns required about 2 months to germinate when planted in a high water-holding medium such as peat moss or vermiculite. Seedling growth was irregular. The formation of buds and the resumption of growth varied with individual plants, irrespective of the temperatures. There was little branching. The plant grown under the 30°C day and 17°C night condition was the tallest as well as the heaviest. All plants had a strong dark brown tap root. Even the lateral roots had a strong tendency to grow downward and consequently the roots were concentrated on the bottom of the container. The root tips were white.

Rhus laurina Nutt.—This native shrub (Anacardiaceae) is confined to lower elevations in the chaparral because of its susceptibility to frost. Germination time for individual seeds varied greatly, even after a pretreatment of soaking in hot water overnight. Increased temperature, either day or night, caused an increase in height, number of nodes, number of branches, leaf size, sugar exudation from leaves, and total dry weight. Each plant had a few thick roots and a dense mat of fine roots. Most of the fine roots were brown and dead. The growing tips of the live roots were turgid and white.

Rhus ovata Wats.—This native shrub, in contrast to *R. laurina,* grows throughout the altitudinal range of the chaparral in southern California. It is less susceptible to injury by cold. To obtain germination, the seeds were pretreated by soaking them in sulfuric acid for 6 hours. High temperatures, both day and night, produced plants with large dry weights, heights, and leaf sizes. A 4°C night temperature practically prevented any growth. Branching occurred only in the largest

plant. The root system was similar to that of *Rhus laurina*.

Salvia mellifera Greene.—A native subshrub (Labiatae) that rapidly invades burns and other disturbed sites (Horton and Kraebel 1955). The seeds germinated well without preplanting treatment. Plants of this species were extremely difficult to transplant successfully. Once established, the plants survived all the temperature conditions except the combination of 23°C day and 26°C night. Under this conditions the leaves became pale green before death. At 30°C day temperatures the leaves also became pale green, but the plants did not die. The cool day temperature of 17°C inhibited growth, but the plants were healthy in appearance. The root system consisted of many fibrous roots with white tips. This native shrub was grown under an additional condition of 23°C day and 10°C night and a 16-hour photoperiod. Eight hours of the night were illuminated artificially at approximately 1,000 foot candles This long photoperiod caused a ninefold increase in dry weight of tops and fourfold increase in root weight.

Exotic species

Baccharis pilularis D. C. ssp. *typica* C. B. Wolf. —A prostrate composite shrub which is native to central California coastal areas (Anonymous 1940). Seeds obtained from the Rancho Santa Ana Botanical Garden at Claremont, California, germinated well without treatment. This normally prostrate plant tended to become upright when grown under a cold night (4°C) in conjunction with warm (23°C) or hot (30°C) day conditions (Fig. 2). All plants branched readily.

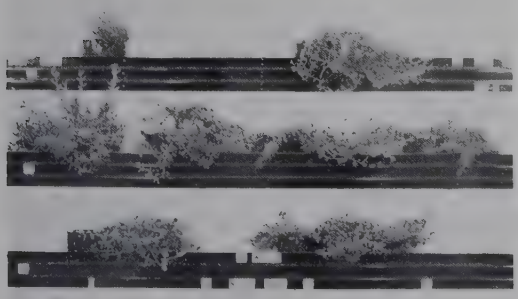

FIG. 2.—Plants of *Baccharis pilularis* ssp. *typica* grown for 6 months under 8 different combinations of day-night temperatures.

The root system was deeply penetrating, and most of the fine roots were concentrated in the bottom of the container. Plants of this species sprout from the roots, and root from the nodes. Field tests indicate that this plant is drought resistant and frost hardy.

Brassica nigra Koch.—Annual black mustard is the seed of commerce used in manufacturing mustard food seasoning. The species is a native of Europe. It is planted in southern California for a soil cover in citrus groves and on fire-denuded watersheds (Gleason 1944; Went 1957). The seeds germinate easily and quickly (Ashby and Hellmers 1955). The plants grew so vigorously that they had to be harvested at the end of eight weeks because of their size. The earliest flowering occurred under the 23°C day and 17°C night temperatures within eight weeks from time of planting. Root nodules developed on the plants grown at the 23°C day and the 17°C and 26°C nights. All plants had a strong tap root with a large number of fine lateral roots that ramified throughout the entire gravel medium.

Bromus stamineus Desu.—This range grass species was introduced into California, presumably from Chile. The seeds germinated quickly without pretreatment. Its growth pattern corresponded closely to that of *Bromus rigidus*. High temperature conditions restricted growth. The largest number of tillers (152) was recorded under the 23°C day and 10°C night (spring-fall) condition. Under all 30°C day conditions and the 23°C day and 26°C night condition the leaves tended to be hairy. The leaves were a light green when the plants were grown under a 17°C day. All plants at the 4°C night temperature flowered, regardless of the day temperatures. The plant at the 30°C day was in flower by 12 weeks, that at the 23°C day by 16 weeks, and that at the 17°C day by 20 weeks. The dense fibrous root system penetrated throughout the medium.

Buddleia globosa Lam.—This shrub (Loganiaceae) is native to Chile. Seeds of this species germinated easily with no pretreatment. Many of the seedlings died when transplanted. Those that survived grew very rapidly and had to be harvested after 8 weeks instead of the usual 24 weeks. The highest temperatures produced the tallest and heaviest plants. Leaves on the greenhouse plants were larger and more succulent than on field grown plants. A definite tap root was formed. The many lateral roots were fine and dark brown except those grown under the 17°C day and 4°C night condition. These latter roots were coarse and almost white. The individual roots were fibrous and strong. In the field, plants of *B. globosa* failed to survive the summer drought.

Calycotome villosa Link.—A shrubby legume, native to the Mediterranean region. The seeds used in these tests came from Israel. Germination

of scarified seeds was 28 percent, compared with 4 percent for untreated seeds. The plant heights, and the dry weights, were restricted by cold nights or cool days. The root systems varied from a single tap root to many coarse main roots. Differences in root systems did not appear to be related to the different temperature conditions. The fine secondary roots were dispersed throughout the container and did not form a mat on the bottom. The roots were light brown, and in the laboratory medium of gravel and nutrient solution they did not form nodules. Plants grown in the lathhouse in soil did form nodules. In the field at 2,800 feet elevation, the plant tops were killed by frost but the plants sprouted from the base of the stem. At the 5,100 foot elevation most of the plants failed after having their tops frozen for two consecutive years.

Cassia acuta Meyen.—A leguminous shrub, native to Chile. The seeds germinated easily without pregermination treatment. Branches grew from almost every node. Under the 17°C day and 4°C night condition, the plants did not grow and finally died during the fifth month of the test. Flowering occurred after 20 weeks under three conditions: 23°C day in conjunction with a 10°C and a 17°C night, and 30°C day and 17°C night. Plants at the 30°C day and 4°C night and the 23°C day and 26°C night had flower buds at the end of the 24-week test period. The root systems consisted of three or more main roots and a mass of smaller coarse brown roots which were concentrated in the bottom of the containers. In the field the plants failed to withstand the drought conditions.

Cneoridium dumosum Hook. f.—This species (Rutaceae) is native to southern California, but it is not found as far north as the San Gabriel Mountains. To obtain uniform germination, it was necessary to stratify the seeds for 2 months at 4°C in moist sand. Cold night temperatures greatly restricted growth. Moderate temperatures induced much branching that caused the plants to have a bushy appearance. High temperatures, 30°C days or 26°C nights, inhibited branching and produced tall slender plants. The roots, both primary and secondary, were coarse, short, and light tan to brown. There were no fine roots. In the field a few plants survived the cold and drought conditions but grew very little over a period of 2 years.

Convolvulus althaeoides L.—This bindweed is native to the Lesser Atlas Mountains of Morocco. Germination percentage was increased by placing the seeds in hot water and allowing them to soak overnight before planting. There were many hard seeds and the best germination obtained, even with a hot water treatment, was only 12 percent. At the high day temperatures of 30°C, plants of this species failed to grow, and died within 4 to 8 weeks. Sprouting from the roots occurred under all the temperature conditions where the plants survived. The root system was composed of fine, white, brittle roots. This species was not field tested.

Cytisus canariensis Kuntze.—A legume native to the Canary Islands. This plant is frequently used as an ornamental shrub in southern California. Between 12 and 25 percent germination was obtained with no pretreatment of the seeds. All plants produced a large number of branches which gave the plants a bushy appearance. The leaves were larger and hairier on plants grown under a 17°C day than those grown under a 30°C day. Plants at all conditions were healthy and strong. Plants at 23°C day and 10°C or 26°C nights were the same height and form, but the lower night temperature produced a plant top that was almost twice as heavy. The primary roots were thick with many fine secondary roots that grew throughout the gravel medium. No nodules were observed on the plants. In field tests the plants grew well and were able to withstand the summer drought and winter frost conditions even at the 5,100 foot elevation.

Dodonaea viscosa var. *angustifolia* (L.F.) Benth.—This shrub grows on dry hillsides in low rainfall sections of Arizona. The seeds germinated easily and required no pretreatment. The height of the plants, and the dry weights, increased under increased day or night temperatures (Fig. 3). Also, leaf length but not leaf width increased with increased day or night temperatures. Under a cold day and night condition the plants survived but failed to grow. For the size of the top, all plants had relatively small short coarse roots. These were white at the lower temperatures, tending toward brown at the higher temperatures. No field tests were made of this species.

Ehrharta calycina J. E. Smith.—A South African perennial range grass, recently introduced into California. The seeds germinated rapidly without pretreatment. The plants tillered under all temperature conditions. The fewest tillers, 71, were produced under the 23°C day and 26°C night condition; the most tillers, 245, were produced under the 23°C day and 10°C night condition. The number of leaves per tiller was fairly constant at four. Flowering occurred under the 17°C day and 3°C or 17°C night conditions and under the 23°C day and 3°C, 10°C, or 17°C nights. The 30°C day temperatures caused the leaves to curl on one edge. The roots were medium to fine

FIG. 3.—*Dodonaea viscosa* var. *angustifolia* grown for 6 months under 8 different combinations of day-night temperatures (°C).

textured for grass roots. They tended toward being brown at the high temperatures and white at the low temperatures. No field tests were conducted with this grass. It has been field grown successfully south of the San Gabriel Mountains (Sampson, Chase, and Hedrick 1951, Jones and Love 1945).

Forestiera neomexicana Gray.—The seeds used in this study were obtained from New Mexico. This species (Oleaceae) also grows in southern California. Here, it occurs on the mountain slopes bordering the desert, an area that occasionally receives summer rain. A pregermination treatment of 2 months' stratification was required to obtain uniform germination. This plant is forced into dormancy by cool day or night temperatures. Day temperature of 17°C and night temperatures of 10°C or lower caused the plants to grow very slowly for approximately 2 months. At this time the plants either formed terminal buds or died. Bud dormancy was broken by heat, irrespective of photoperiod. The plants did not branch. The root system consisted of a tap root with many fine, whitish lateral roots along its entire length. In the field, most of the plants survived the drought. Height growth varied inversely with the depth of soil. The plants could not withstand the cold winters of the 5,100 foot elevation.

Lolium multiflorum Lam.—An annual grass introduced from Europe and used extensively in California for range reseeding and for winter lawns. This plant also has been used to produce a quick cover after wildfire burns in southern California (Went 1957). Seed of this species germinated rapidly without any pretreatment. This very vigorous species tended to have a sprawling growth habit. Plants under all conditions tillered profusely, having more than 500 tillers on even the smallest plants. The numerous fibrous roots that spread throughout the containers tended to grade from coarse to fine under increasing temperature conditions.

Lotus bertholetii Masf.—A prostrate legume, native to Cape Verde and the Canary Islands. Plant material used in this study was rooted cuttings from a shrub on the campus of the University of California at Los Angeles. At low day and night temperatures the many stems were thick and leafy (Fig. 4). Spindling plants were produced at the higher temperatures. This was especially noticeable under the 30°C day conditions; the stems were thin and had few leaves. At the end of the study (6 months), plants growing at the 17°C day and 4°C night had formed flower buds which were opening. The roots, like the stems, were of finer texture under the higher-temperature growing conditions. Root nodules were formed on plants grown in soil in the lathhouse but no nodules were formed on plants grown in the sterile medium of the laboratory. In the field the plants could not withstand the summer drought. Furthermore, when the plants were not protected they were browsed.

Lotus mascaensis Burch.—A dwarf shrub, native to the Canary Islands. Seed of this legume germinated rapidly and well. The first plants appeared 3 days after planting, and within 3 weeks 100 percent germination was attained. Growth of the plants was markedly changed by the different temperature conditions. The coldest condition, 17°C day and 4°C night caused the plants to be prostrate, dark green, and to have short internodes. Moderate day temperatures (23°C) produced sprawling plants, whereas a 30°C day temperature produced upright plants. The color of the leaves was lighter and the internodes longer with increased temperatures. All plants were greatly branched. At the end of 6 months, plants at 23°C day and 10°C night temperatures had flowered while plants at 23°C day and 4°C night were in bud. The root systems had several large deep-penetrating roots and many fine secondary roots. The fine roots spread throughout the gravel medium. As with *L. bertholetii*, nodules were produced on plants grown in soil in the lathhouse

but not in the sterile medium of the laboratory. Field plantings failed to survive the summer drought.

Lygeum spartum Loeff.—This grass is a native of Spain, where it is used in the production of commercial fibers. The seeds germinated within 2 weeks, often producing several plants per fruit. In general the plants grew more slowly than the other grasses tested. Cold nights greatly inhibited growth and the number of tillers formed. Nine tillers were produced at the 23°C day and 4°C night compared with 21 to 45 tillers at the same day temperature and a 10°C night. There were usually 3 leaves per tiller. The root system of each plant consisted of a few small white roots. Three years of field tests showed that while the plants were capable of surviving the drought and frost, they grew very slowly and did not spread.

Phalaris tuberosa var. *stenoptera* (Hack.) Hitchc.—This perennial range grass, locally called Harding grass, was introduced from South Africa. It is used in California in seeding irrigated pastures and on deep soil sites (Sampson, Chase, and Hedrick 1951). The seeds did not require any pregermination treatment. Plants at the lower temperatures had a flat and spreading habit and the culm bases were purplish. One hundred and ninety-eight tillers were produced under the 23°C day and 10°C night condition. In contrast, only 61 tillers were produced under the same day temperature and a 26°C night temperature. Under the 30°C day temperature conditions many of the basal leaves had died by the end of the 6-month test period. The root system was large and composed of many branched roots. At the lower temperatures there were many large white roots and some darker, finer roots. At higher temperatures there were fewer large white roots, and under both 30°C day conditions most of the roots were dark and fine. This grass was not field tested.

Pinus brutia Ten.—This tree is also known as a variety of *P. halepensis*. *P. brutia* is native to southeastern Europe and western Asia. The seed used in the laboratory test came from Cyprus. Untreated seed germinated in about 6 weeks. A month of stratification at 4°C shortened the time to germination and increased the percent of germination. Height growth was favored by the 23°C day temperature and 10°C and 17°C night temperatures, and by the 30°C day temperature and 17°C night temperature. All of the plants grew continuously during the 6-month period without forming terminal resting buds. At the end of the experiment the plants were still producing juvenile growth with a few fascicles of needles. The plant at the 17°C day and 17°C night formed fascicles in 20 weeks. All the plants were branched. The roots were coarse and brown with thickened white tips. Plants from three seed sources were grown in soil in a lathhouse. Larger plants were produced from Italian and Turkish seed than from Cyprus seed. A field test, using plants grown from seed obtained from Cyprus, Italy, and Turkey, was established. Several plants from the Cyprus seed failed to survive under field conditions.

Retama raetam Webb and Berth.—A shrubby legume found in the Mediterranean region. Seed source for this lot was Israel. A pregermination treatment to break the seed coat is necessary to obtain good germination. Cutting the seed coat with a file or treating it with concentrated sulfuric acid for 5 hours resulted in about 90 percent germination. The plants of this species were relatively slow growing compared with the majority of species tested. At the higher tempertures the plants were taller but had fewer branches. All plants had but few leaves. The leaves were larger and more persistent at the cooler temperatures. The root system consisted of a tap root with relatively few fine secondary roots. These secondary roots tended to form a mat on the bottom of the container. Root nodules were formed when the plant was grown in soil in the lathhouse. Plants of this species that were put in the field failed to survive freezing temperatures.

Schinus dependens Ort.—This shrub or small tree (Anacardiaceae) is native to Chile. The seeds required 5 weeks to germinate. Plant heights were greater at the higher temperatures. The leaves stood out from the plants and were parallel to the ground under the lower temperatures. Under the higher temperatures the leaves drooped. The plants had tap roots from which relatively large white lateral roots developed. These were formed just below the ground surface. The small roots were dark brown in color. In the field the young shoot tips were frozen, but the plants were not killed. The plants withstood the extreme drought conditions.

Sophora tetraptera Ait.—The seeds of this shrubby legume came from Chile. A combination of hot-water treatment and puncturing the softened seed coat before planting was necessary to obtain germination. Height growth, like dry weight, was greatly reduced by the 4°C night, the 26°C night, and the 30°C day conditions. There was no branching under the 4°C night condition. The relatively sparse root system was tan in color and consisted of a tap root with coarse laterals. No root nodules were observed on plants grown either in the sterile medium or in soil. This species was killed by the cold and drought conditions when field tested.

Spartium junceum L.—A leguminous shrub found in the Mediterranean region. Our seed came from Israel. The seeds germinated readily without any pretreatment. Temperature affected the form and leaf retention of the plants. The plants grown at a 30°C day and 4°C and 17°C nights and at a 23°C day and 26°C night were weak and did not stand erect. The plants grown at cooler temperatures had shorter and thicker stems which were able to support their own weight. Leaves were retained on the plants grown at the 17°C day and 4°C and 17°C nights and at the 23°C day and 4°C night. At higher temperatures the leaves dropped soon after they were formed. All of the plants produced relatively few and small leaves, but the stem remained green. The plants were branched and had a very bushy appearance, especially at all temperatures higher than the 17°C day and 4°C night condition. The roots were branched and permeated the entire medium. Root nodules were formed on the plants grown in soil in the lathhouse. This species has been planted along highways in the mountains of southern California for more than 20 years. It survives and grows well on road fills and occasionally in road cuts, but it has not been able to invade the adjoining stands of chaparral.

Zizyphus lotus Lam.—A spiny shrub (Rhamnaceae) which grows in the Mediterranean region. Seed source for this lot was Israel. The seeds had to be removed from the fruit and their hard shell before they would germinate. The seeds germinated within 4 weeks. Growth of these plants was greatly inhibited by all but the highest day and night temperatures. The plants died after 16 to 20 weeks at the lowest temperatures (winter). There was little terminal growth at any temperatures except the 23°C day and 26°C night condition. The plants had a strong tendency to develop branches. Successive branches showed much vigor when they first developed, but the vigor soon decreased. Under all 17°C day conditions and all night conditions below 17°C, the older branches soon lost their leaves and died. The plants formed a tap root. Most of the very white and brittle secondary roots were concentrated in the bottom of the container. This species was not field tested.

Zizyphus nummularia DC.—A spiny shrub, native to India. In appearance and growth this shrub is similar to *Z. lotus*. The seeds germinated well if their hard outer shells were removed. Forty percent germination was obtained within 1 week, and germination increased to 68 percent within 15 days after planting. Like *Z. lotus, Z. nummularia* tended to form greatly branched plants, was not able to survive the cold winter conditions, and had a tap root as well as white and brittle secondary roots. In contrast to *Z. lotus, Z. nummularia* did not exhibit rapid growth under the 23°C day and 26°C night temperature conditions but did grow better under the 23°C day and 10°C and 17°C night temperature conditions. This was one of the last species grown and was placed under the additional condition of a 23°C day and 10°C night with a 16-hour photoperiod. The long photoperiod had no effect upon the size of the top of the plant, but it increased the size of the root system threefold. This species was not field tested.

FIG. 4.—*Lotus bertholetii* grown for six months under 8 different combinations of day-night temperatures.

DISCUSSION

The most critically eroding sites in the San Gabriel Mountains have little or no plant cover. This lack of cover exposes the ground to maximum insolation during the day and permits maximum radiation during the night. Thus the climatic conditions on these sites are the extremes for the area, and knowledge of a plant's growth capabilities is essential in making selections for erosion control plantings.

The combination of a 6-month growth study under controlled temperature conditions and a field test for drought and frost resistance furnished the needed information for screening the exotic species. The advantages of the laboratory test were threefold. First, the temperature effect upon plant growth was isolated from other factors, such as moisture, insects, or soil fertility, that may affect growth in the field. Second, the time required for testing was relatively short. A field study covering a comparable range of temperature conditions under the irregular temperature pattern that occurs in southern California would have required nurseries at different elevations operated over a period of many years. Third, the laboratory study was more economical in both man-

power and money than an extensive field nursery program. The conditions for a field test for drought and frost resistance occur annually and are easily obtained. Based on the results of the laboratory findings, it was necessary to field test only a relatively small number of the species.

Of all the species tested, *Baccharis pilularis* ssp. *typica* is outstanding as a potential plant for use in erosion control work in the San Gabriel Mountains. Use of suitable species to protect the bare, rapidly eroding slopes can bring about soil improvement. The better site quality resulting may lead to invasion of other species. These species in turn may be desirable, or management of the area may be needed to exclude them from the plantings.

Plants of *Baccharis* grew exceedingly well even under the most extreme conditions of laboratory and field tests. Furthermore, the plant roots at the nodes, is prostrate, and covers a relatively large ground area for the amount of plant material produced. It also spreads by sprouting from the roots. These factors are of major importance in the San Gabriel Mountains, where total plant growth is limited by lack of soil moisture and by a low level of plant nutrients.

Cytisus canariensis, Calycotome villosa, and *Spartium junceum* were the best of the tested legumes. Although these species were not tested for nitrogen-fixing ability, nodules were observed on the latter two species. Even though these small-leafed shrubs are erect in form and are of little value as cover plants, they might be advantageously used as soil builders in mixed stands. At least further field testing is warranted to determine their ability to grow in, and to improve the growth of, mixed stands of native or exotic species.

The exotic annual grass *Lolium multiflorum* and the annual mustard *Brassica nigra* are both capable of growing under the cool conditions of southern California winters. Both species, either singly or mixed, are now being used to sow wildfire burns. The objectives of such sowings are (1) to obtain a plant cover on denuded mountain slopes as quickly as possible after the first fall rains, and (2) to maintain a protective cover during succeeding years until the native shrubs again dominate the area.

No doubt plant species other than certain of those tested could be successfully and advantageeously grown on San Gabriel Mountain slopes. Our selections for testing were based on the rather limited information available on wild species, and some highly desirable species may have been omitted. Some species, suggested as the present study was drawing to a close, could not be fitted into the tests reported here. Two such groups of plants that seem worthy of further study are the Cistus species and brush species of Atriplex which are native to the Mediterranean region.

Ecological Implications

An understanding of some of the autecology of the individual species resulted from the laboratory study. In some species it is very evident that optimum plant growth is dependent upon the temperatures that occur in the native habitat when water is available. It must be emphasized that the relationship is between temperature and available water, and not necessarily the rainfall pattern.

The growth pattern and distribution of two native chaparral species in the San Gabriel Mountains of southern California exemplify this temperature-moisture relation. *Rhus laurina* grows best under high temperatures. In the field this shrub grows at low elevation, and on frost-free slopes with deep soil where warm temperatures occur early in the year when water is available for plant growth. It also occurs in areas such as stream channels, alluvial cones, and on sites in the coastal fog belt, where there is available moisture into the late summer. *Adenostoma fasciculatum,* on the other hand, grows under the low temperatures of early spring and is inhibited by high temperatures. In the field this shrub is dominant on the hot, dry south-facing slopes. On these slopes moisture for plant growth is limited to the cool rainy season. The shallow soil, underlaid by fractured rock, has a very low water-holding capacity, and once the rains cease, the available moisture is quickly depleted.

Many exotic species also had a growth pattern that fitted into the seasonal distribution of temperature and soil moisture in their native habitats. *Dodonaeae viscosa* var. *angustifolia* grew best under high temperatures and went dormant under low temperatures. This growth pattern fits the rainfall distribution of Arizona, where the seed was obtained. Even though parts of Arizona have a low average yearly rainfall, much of it comes in summer thunderstorms. These make water available for plant growth during the hot summers.

Zizyphus lotus is another shrub that requires high temperatures for growth. In its native habitat around the Mediterranean it is a deep rooted shrub that grows in loess and grey calcareous soils having a high water-holding capacity (Feinbrun and Zohary 1955). Moisture retained in these soils is probably the source of water for plant growth during the hot, rainless summer.

Lotus bertholetii is a plant that grows best under moderate to low temperatures and is retarded by high temperatures. Even though this species

is native to the Canary Islands, which have a Mediterranean-type climate, it does not grow on hot dry sites. The plants are found only in a small area on the northern side of the main islands (Ceballos and Ortuno 1951). During the summer months the prevailing northeast trade winds bring moist air that rises against the side of the mountain, causing cloud formation and rainfall. *Lotus bertholetii* is found in the cliffs on damp sites that in the summer are shaded and kept moist by the cloud layer. During the summer the rest of the island is subjected to the hot dry weather typical of a Mediterranean climate.

Summary

The present study was conducted to test the adaptability of exotic species for use as erosion control plants in the San Gabriel Mountains of California. The climatic conditions of cool, wet winters and hot, dry summers greatly restrict the selection of otherwise suitable plants. The most promising species found through a literature search and through contacts with biologists in other regions of the world with a similar climate were tested. Selected plants were grown under eight sets of day and night temperature conditions including seasonal average day and night temperatures of the mountains. Twenty-four exotic species were tested, and eight native species were grown as controls. Many of the exotic species were field tested to determine their frost hardiness and drought resistance.

Plants grown in the laboratory showed marked differences between species in temperature requirements for survival and growth. These differences were present between the native as well as the exotic species.

Results of the growth, frost-hardiness, and drought-resistance tests made it possible to select the species most adapted for survival and growth in the San Gabriel Mountains. One species, *Baccharis pilularis* ssp. *typica,* appeared to be outstanding because, in addition to good survival and growth, it was prostrate and rooted at the nodes. Three well adapted leguminous species, namely, *Cytisus canariensis, Calycotome villosa,* and *Spartium junceum,* appear desirable because of their soil-building possibilities rather than because they were particularly good cover plants.

An understanding of some of the autecology of the individual species was obtained from the results of the study. For some species it is evident that optimum temperature for plant growth is closely related to the temperatures that exist in the species' native habitat when water is available.

Acknowledgments

The authors wish to thank Dr. F. W. Went for his cooperation in establishing many of the foreign contacts and for his assistance and guidance throughout the entire study. We wish also to thank the many biologists around the world that cooperated on this project by offering suggestions and supplying seeds. Unfortunately, time and laboratory space prevented us from testing all the species we received.

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FIELD EFFICIENCIES OF FOREST SAMPLING METHODS

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INTRODUCTION

In comparing the field efficiencies of various forest sampling techniques on an equivalent basis, the large number of each kind of unit required for a thorough statistical analysis makes direct use of a natural stand impractical. The use of a two-dimensional model or map of an actual forest has certain advantages over either the stand itself or an artificial laboratory population. It is desirable that the stand be mature and practically undisturbed by man. Further advantages accrue to a stand which had been reported on previously by ecologists and is permanently protected for possible future study. The stand selected, which has these features, is the 20-acre central portion of 80 acres of undisturbed forest (Donaldson's Woods) in Spring Mill State Park, Lawrence County, Indiana. Our primary purpose was to determine the field-statistical efficiencies of forest sampling methods, with emphasis on the more rapid recent ones, and to evaluate the usefulness of each for forest analysis. The study yielded also a description of the tree stratum of this 20-acre tract after the lapse of the several periods of time since the less detailed studies of Donaldson's Woods by Record (1906), Cain (1932), and Braun (1950). This result was a by-product of the sampling work; a complete phytosociological study was not attempted.

Oosting (1956) stated that the major concern in sampling is to get adequate information with a minimum of effort. Cottam and Curtis (1956), in discussing the evaluation of methods, wrote, "Probably the most important factor is the time required to obtain an adequate sample."

New methods and modifications have been tested in various forest types against full tallies and standard quadrat methods (Cottam and Curtis 1956, Husch 1955, Lindsey 1955, Rice and Penfound 1955, Shanks 1954, Sudia 1954) and against artificial populations (Cottam, Curtis and Hale 1953, Penfound 1945). Borman (1953) and Johnson and Hixon (1952) have tested quadrat size and shape using complete censuses.

In a study of size requirements for mixed forest in Illinois, Vestal and Heermans (1945) included an old growth stand having 125 trees per acre,

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very close to the 123 we found in Donaldson's Woods. These workers concluded that in such woods 20 acres is the "definitive area" which dependably characterizes the type as to species present, order of abundance and of basal area per acre, and in general range of sizes of the trees of each species.

Donaldson's Woods occupies the W. ½ of the N. E. ¼ of Section 4, T. 3 N.; R. 1 E. of the Second Principal Meridian, Mitchell Quadrangle. No lumbering has occurred in the stand. A few dead or windthrown trees were removed by the Civilian Conservation Corps in the early 1930's, according to Mr. William Overlease, Park Naturalist, and Roscoe Baldwin, Park Staff. This explains the few old uprooted cut stumps found there today. Fire damage has been very slight; there has been no report of serious fire occurring since some time prior to 1906 (Record 1906).

The area lies within the unglaciated south-central part of Indiana, on the karst topography of the Mitchell plain. The basic bedrock is Mississippian St. Louis limestone of the Lower Mitchell Limestone Series. Shallow closed sinkholes separated by low broad divides characterize the physiography. The limestone-derived soils were mapped as Frederick silt loam, shallow phase (Tharp, Bushnell, and Adams 1922). Later, the Orleans soils have been separated. Prof. H. P. Ulrich suggested (personal communication, 1956) that these slopes would now be mapped as Orleans.

The nearest meteorological station reporting to the U. S. Weather Bureau is 10 miles north, at Bedford, Indiana. Data from another station, at Paoli 13 miles south of Spring Mill, were combined with the Bedford records to obtain averages assumed to approximate general climatic figures in the region of the stand. The annual precipitation so calculated is 42 inches, the mean annual temperature, 55°F. The frost-free period is 160-180 days. The average number of cloudy days annually is 125. The normal temperature for June, July, and August combined is 72°F., and for December, January, and February it is 33.7°F. The normal precipitation for the 3 summer months is 3.4 in. and for the 3 winter months 3.3 in. (U. S. Weather Bureau, 1955).

The writers are grateful to the Purdue Research Foundation for a grant to the first-named author. The Indiana Department of Conservation granted permission to work on state-owned land. Field work by the two first-named authors was carried on in the summer from 1954 through 1956. A preliminary part of the work was reported in an unpublished thesis by Barton (1956), and the project was continued by Miles and Lindsey into 1958. Field timing was done by Lindsey with the assistance of David K. Sterling.

The Full Census and the Map

A rectangular area of 20.145 acres, 1300 ft. north-south by 675 ft. east-west, was surveyed by transit, and permanently marked by steel rods at the corners. A contour map and detailed corner diagrams are given by Barton (1956) for locating the permanent markers. The area was divided into 13 adjacent strips 675 ft. by 100 ft., surveyed by transit along the center of each strip and marked temporarily by east-west string lines. Later, raw data for mapping the stand were recorded in the columns of engineers' field level books, as follows. A 200 ft. steel tape marked in feet was stretched beneath the center string. One of the two workers would walk westward along the tape to the point where a horizontal line from a tree north (or south) of the tape intersected the tape perpendicularly. He would then record the direction ("N." or "S.") of the tree and its distance along the center tape from the base line (eastern boundary). The other worker would call out the species and its diameter-tape reading (d.b.h.), to be recorded. By use of one 50 ft. tape, both workers would then measure the distance from the strip center line to the center of the tree. Trees nearly 50 ft. away were marked with yellow lumber crayon to prevent duplication in an adjacent strip. No stems less than 4 in. d.b.h. were recorded. A right-hand column was reserved for later office tabulation of basal areas, using a different color pencil for each species.

The tree population was mapped in India ink on drafting linen on a scale of 1:36. (The large scale facilitated strip and Bitterlich sampling.) The tree centers were plotted at the equivalent scale distance along and out from the center lines drawn on the map. Circles indicating approximate basal areas were drawn in 3-in. size classes, for later variable-radius sampling from the map. The abbreviation of the species name, the d.b.h. in inches and tenths, and the basal area in square feet (to 4 decimal places) were placed adjacent to each tree trunk circle. Ozalid copies of the 20-acre map were made. The original is in the plant ecology laboratory at Purdue University.

For both density and basal area by species and size classes, careful full tallies, repeated several times, were made from the unassembled map sheets; the resulting data were considered as the true population values, for comparison with both field sampling and assembled map sampling (Fig. 1) results. Figure 2 shows a stand diagram and a tabular breakdown into size classes, on the basis of the first general count made. It is slightly less

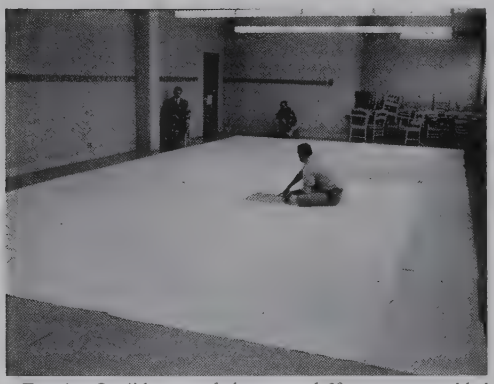

FIG. 1. Ozalid copy of the map of 20 acres, assembled for sampling. Photo by John Merkle.

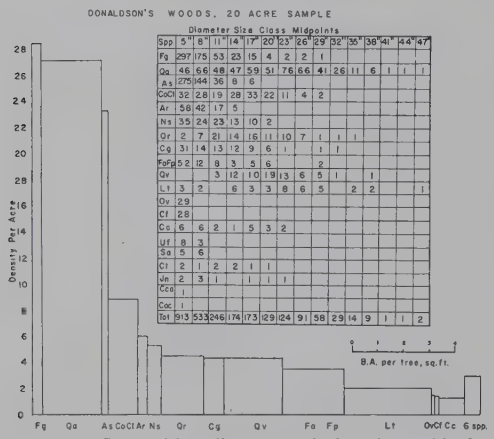
DONALDSON'S WOODS, 20 ACRE SAMPLE
Diameter Size Class Midpoints
Density Per Acre
B.A. per tree, sq.ft.
Fg Qa As CoCl Ar Ns Qr Cg Qv Fa Fp Lt OvCf Cc 6 spp.

FIG. 2. Composition diagram and size class table for trees at least 4″ d.b.h. in 20 acres of Donaldson's Woods. Height of rectangle shows number of stems per acre, width shows mean basal area per tree, and area of rectangle represents basal area per acre. Fg symbolizes *Fagus grandifolia* Ehrh. (beech), Qa *Quercus alba* L. (white oak), As *Acer saccharum* Marsh (Sugar maple), Co *Carya ovata* (Mill.) K. Koch (shagbark hickory), Cl *Carya laciniosa* (Michx. f.) Loud. (shellbark hickory), Ar *Acer rubrum* L. (red maple), Ns *Nyssa sylvatica* Marsh (black gum), Qr *Quercus rubra* L. (northern red oak), Cg *Carya glabra* (Mill.) Sweet (pignut hickory), Fa *Fraxinus americana* L., Fp *Fraxinus pennsylvanica* Marsh. (green ash), Qv *Quercus velutina* Lam. (black oak), Lt *Liriodendron tulipifera* L. (tulip tree), Ov *Ostrya virginiana* (Mill.) K. Koch (hophornbeam), Cf *Cornus florida L.* (flowering dogwood), Cc *Carya cordiformis* (Wangenk.) K. Koch (bitternut hickory), Uf *Ulmus rubra* Muhl. (slippery elm), Sa *Sassafras albidum* (Nutt.) Nees (sassafras), Ct *Carya tomentosa* Nutt. (mockernut hickory), Jn *Juglans nigra* L. (black walnut), CCa *Carpinus caroliniana* Walt. (American hornbeam), and Coc *Celtis occidentalis* L. (hackberry).

accurate than the later counts tabulated below, but these were not by size classes.

For compactness in the tables and text, common names are used; the legend for Figure 2 shows the corresponding technical names. Shagbark and shellback hickories were tallied as though they made up a single species. White ash and green ash were likewise tallied together. None of these four was used for the principal statistical comparisons in this paper.

The two largest individual trees were white oak and tulip tree, both 47 inches d.b.h. (Fig. 2). White oak is the second most abundant species, while tulip tree is one of the least abundant of the canopy species. The most abundant species, beech, attained a maximum of 29 inches d.b.h in the 20 acres studied.

While white oak averaged 18.7 inches d.b.h. and tulip tree averaged 22.1 inches d.b.h., beech averaged only 7.5 inches d.b.h. There were only 3 other species that exceeded the largest beech—red oak, pignut hickory, and black oak. The third most abundant species, sugar maple, averaged a little less than beech, but had a distinctly lower maximum of 17 inches d.b.h. (No trees below 4″ d.b.h. were included.)

Three species, beech, white oak, and sugar maple, had comparatively high density per acre (Table I); all were about equally represented (23-28). These 3 species made up 64 per cent of the trees over 4 inches d.b.h. Two other species made up an additional 12 per cent of the total—red maple approximately 7 per cent, and the shagbark hickory group approximately 5 per cent. Tulip tree, conspicuous because of its great average size, contributed 1.6 per cent of the population of 123 trees per acre. Black gum and red oak bring the total to 84 per cent contributed by the 7 most abundant species.

TABLE I. True population values,[1] for the species utilized in the analyses, derived from complete census of 20.14 acres of Donaldson's Woods

Species	Density per acre (D_2)	Basal area per acre (B_2) in sq. ft.	Relative density (D_3)	Relative basal area (B_3)
Beech.....	28.29	10.28	23.0	8.3
Sugar maple.	23.33	6.12	18.9	4.9
White oak...	27.25	62.98	22.1	50.6
Black gum...	5.26	3.05	4.3	2.4
Tulip tree...	1.99	5.96	1.6	4.8
All 22 species	123.16	124.50	100.	100.

[1]The four parameters are in the sense commonly used, and as defined by formulae in an earlier paper (Lindsey 1956). Only stems 4 in. d. b. h. or larger are included.

Basal area presented a different picture of the status of certain species. White oak with 63 square feet per acre made up 50 per cent of the population total. The next species was beech with 10.3 square feet per acre or only 8.3 per cent. Shag-

bark hickory is fifth in density, but about equal in basal area with beech. The 3 species comprised 66 per cent of the total basal area. This is comparable to the 64 per cent, of the total number of trees, contributed by beech, white oak, and sugar maple. The red and black oaks supplied 6 per cent each, and the sugar maple and tulip tree 5 per cent each, in basal area.

Thus approximately 89 per cent of the basal area was contributed by the first 7 species, 2 of which, tulip tree and black oak, were not represented in the first 7 most abundant species.

Cain (1932, p. 114) reported that 4.45 per cent of the trees over 4 inches d.b.h. were tulip trees. This was estimated from twenty-five 10 x 10 meter quadrats. From both this quadrat size, and from long narrow strips giving 10 per cent survey, Cain found white oak, beech, and sugar maple in nearly equal numbers starting with 1 inch d.b.h. He reported that trees over 4 inches d.b.h. were approximately 36 per cent white oak, compared with 22 per cent in the present study. This difference is less likely due to real changes during the 25-year period than to the imperfect comparability of the two sets of data.

The Braun (1950), Cain (1932), and Record (1906) data compared with the present study indicate beech and red maple are increasing in the size classes above 10 inches d.b.h. Beech of this size has increased progressively in relative density from 1906 (3 per cent), to 1932 (5 per cent), to 1956 (8.5). Red maple over 10 inches was unreported by Record or Cain, Braun found it as 0.6 per cent, and we found 2.1 per cent. White oak has held its prominent position for the last 50 years. No black oak were recorded between 4 and 10 inches in diameter in this study; reproduction of this species is poor. Since the older studies are based on the 80 acre woods with relatively low sampling intensity, while ours is a complete census of a 20-acre portion only, conclusions about changes must be considered tentative.

As Braun (1950, p. 143) points out, Donaldson's Woods does not appear to be climax and represents a transitional mixed group, between mixed-mesophytic and oak-hickory.

An investigation regarding the distribution of number of trees by diameter classes showed that Donaldson's Woods conformed fairly well to the balanced uneven-aged forest structure described by Meyer (1953). The average ratio of number of trees in successive diameter classes (Meyer's "q") was approximately 1.5. It is interesting to note that when the stand was analysed similarly but excluding all species of oak, the correspondence to a balanced uneven-aged structure was much closer. The size-class table in Figure 2 shows that within the oak species the trees are distributed much as we might expect an even-aged forest to be, that is with high frequencies near the mean diameter and tapering off both above and below. (This paragraph was supplied by Thomas W. Beers).

Braun (1950); Potzger, Friesner and Keller (1942); Cain, Friesner, and Potzger (1930); and Freisner and Potzger (1937) indicate that in southern Indiana generally oaks and hickories occupy the ridge tops and dry southern exposures. Beech and maple tend to dominate the lower slopes and moist northern exposures. Neither Braun nor Cain has indicated that any zonation existed in Donaldson's Woods. If present it was too subtle to be readily apparent, although it might be suspected from the array of species. For example, black oak, usually associated with higher topographic positions, contributes 3 per cent of the density and almost 7 per cent of the basal area. Beech and maple combined make up a large portion (42 per cent) of the density although not much more than black oak in basal area.

In order to investigate the importance of topographic zonation present, 80 fifth-acre quadrats taken from the map were sorted into 25 the centers of which fell on the lower slopes and sinkhole bottoms, and 55 with centers on the ridges and upper slopes. Basal area per acre was definitely greater in the sinks for beech, shagbark hickory, red maple, gum, red oak, ash, tulip tree, false pignut hickory (*Carya tomentosa*), and bitternut hickory (*Carya cordiformis*), and less for white oak and black oak. Little difference is noted in sugar maple, pignut hickory, and the less abundant subdominant species. Density for sinks as opposed to uplands is greater for shagbark and shellbark hickories, red maple, gum, and tulip tree. The sinks have fewer trees per acre for beech, pignut hickory, and black oak in the canopy trees, and ironwood (*Ostrya virginiana*) in the lower tree strata. Little difference is noted for white oak, sugar maple, and ash among the canopy species, and most of the subdominant species. Thus it appears that some differentiation due to topographic position is present in Donaldson's Woods although it is not readily perceived by field inspection. Presumably this is correlated with differences in soil moisture.

The greater density and basal area of the oaks and the hickories on the upland, with the fact that black oak is not reproducing as well as it must have at some earlier time, indicates that probably this differentiation was more pronounced earlier than is evident now. This also indicates a trend

on the upland toward a more mesophytic forest type than in the past, even though Donaldson's Woods is as close to a virgin forest as remains in Indiana. When viewed in the light of earlier studies, this trend could account for the good survival of beech and maple and for their apparent increase in 50 years. Such a change indicates successional advance; climatic change is said to have gone in the opposite direction, toward slightly more xeric climate.

A few small slippery elms were found; all of these were less than 10 in. d.b.h. Dogwood and ironwood were conspicuous in the small tree stratum. An occasional sassafras marks a previous canopy opening that has since been occluded. Black walnut reached relatively large size (maximum tallied 23 inches d.b.h.), but averaged only one-half tree per acre.

The Basis of Efficiency Comparisons

Comparison of field efficiency among methods should be based on the time required in the field to attain an equal level of sampling adequacy. A 15 per cent standard error has been selected as the constant adequacy level required in the present study. The most efficient method is the one that yields this standard error in the shortest time. The number of sample units, and, hence, trees irrespective of species, necessary for this level was determined from intensive sampling of the 1:36 scale map. The time needed for sampling this number of units and trees comprises two components—operating time at the units, and time walking the circuit of the required number of units in the field. The more units are required, the longer the zig-zag course among the stratified-random units, and the greater the total inter-unit time.

For a given method the number of sample units required for 15 per cent standard error was multiplied by the average number of trees, irrespective of species, per unit. The product, total number of trees required, was multiplied by the average time per tree, in seconds, and this product was divided by 3600 to give hours of time-within-units needed to obtain 15 per cent standard error. To this working time at the units was added inter-unit walking time determined from a small index map. The sum was termed "field time" for the particular method, and is an inverse measure of its "field efficiency"; high time values signify low efficiency.

Different species, requiring different numbers of units for adequacy, gave different field time results. Other things being equal, the higher the density of the species the shorter the time needed. Although statistical analyses were made for all methods for 7 species, only the beech and maple were utilized for determining sampling efficiencies.

Time Per Tree at the Sampling Units

In timing the procedure at each point or plot, the same two-man crew worked in the field with all methods. Only that part of the method applicable to the tree stratum was considered. The object was not to establish maximum speeds, but to carry out the methods at rates which could be maintained steadily throughout the day without strain. The crew had had most prior experience with the strip method and full Bitterlich methods; it was about equally experienced with each of the other methods, in the particular ways in which they were performed. The order of use of the various methods at a given point was rotated for successive points.

In a given sampling method, minor differences in procedure may make a marked difference in the time required. Also, newer modifications of most methods have increased their speed and ease of operation. It is essential, therefore, to report exactly how each method was carried out when timed in the field, for determining the time per average tree. Determination of time per adequacy standard was derived in part from this.

Except for the strip, all methods used herein require establishment of points in the stand, each to serve as the center of a sample unit. This applies to the quadrat methods as used, as well as to the newer point methods. The methods which tally more trees per unit require fewer units for the same level of sampling adequacy. To keep the methods used as comparable as possible, only methods yielding both absolute (per acre) and relative density and basal area were included. The augmented variable-radius method (Rice and Penfound 1955), which gives accurate density results in per cent figures only, was not included.

Square plots

The most rapid method known to us for laying out square plots requires a Brunton pocket-transit leveled by bubble on a Jacob's staff set at the center point of the quadrat, and a steel tape of sufficient length to stretch over the diagonal of the size square used. One man at the point sights through the arms of the Brunton compass and holds the reel of the tape while directing the second or flag man along a straight diagonal line as that worker walks out with the tape end and one flag. Bright-colored adhesive tape fastened around the steel tape facilitates the measurement, which is the diagonal halved. The half-diagonal is 66 ft. for a fifth-acre square, 46.6 ft. for a tenth-acre, 29.6 ft. for a twenty-fifth acre, and 23.3 ft. for a

fortieth-acre plot. The far end of the half-diagonal line becomes a corner of the square.

At the proper distance out, the flag man sticks into the ground a 2 ft. metal pin to which a cloth flag has been affixed; on his return past the center point he receives from the point man the reel and another flag. He places the latter at the opposite end of the same diagonal, assisted by the point man's holding the proper half distance mark of the tape. The flag man then winds up the tape on the reel and walks to the point, while the other turns the compass 180° and stabilizes it. The flag man hands the reel to the point man and takes the end of the reel out along the alternating diagonal, repeating as before. When the four flags are placed, the point man records species and diameters called by the other, but also, whenever possible, himself measures and records trees from the opposite corner. During this operation, both men take up the corner flags as they are no longer needed. No boundary cords are laid out in this method.

Five of each size of these square plots were timed. The fifth-acre ones required only 31.8 $\pm$ 3.36 seconds per tree, with a coefficient of variation of 24 per cent. The tenth acre squares took 41.5 $\pm$ 3.22 seconds per tree with a *CV* of 17 per cent, while the twenty-fifth acre plots took 65.1 $\pm$ 9.66 seconds per tree, and had a *CV* of 33 per cent.

A trial of one-fortieth-acre quadrats laid out by diagonals shows that this size was too inefficient to use by this method, in terms of time per tree (77 seconds). The same size square with the boundaries marked out on all four sides by a white plastic clothesline with loops at the corners for metal pins, was also tried and abandoned. Much time was consumed in reeling and unreeling the line on a large metal spool, and in squaring up the plot when the last side fell short, or overlapped the first. Without a reel, dragging the 132 foot line through the woods lengthwise between sampling sites speeds the method somewhat for making one-fortieth-acre plots, but for tenth-acre or larger ones the bulk of the reeled line or the length of the unreeled line would render the method impracticable. In special cases, as for small quadrats in thickets with poor visibility the method might be more suitable.

Circular plots

By using a 6-inch base Edscorp rangefinder from the point, circular plots of two sizes, one-tenth and one twenty-fifth acres, were surveyed without the need of laying out boundaries. As in Bitterlich sampling by angle gage, one worker stands at the point, starts with the nearest tree (or the first trunk to the right of the sun), and rotates through 360°. Unlike the Bitterlich method, the man at the point does all the recording; he has little sighting to do because for most trees it is obvious without the instrument whether they are in or out. The other man measures each included tree (4 in. d.b.h. and over) by diameter tape, calls the figures, and assists in identification.

For tenth acre plots, the aluminum dial of the rangefinder was scratched at 37.2 ft.; another mark at 23.6 ft. indicated the radius distance bounding the twenty-fifth acre plots.

The 16 plots of twenty-fifth-acre area gave an average time of 20.0 $\pm$ 1.75 seconds per tree, the plus-minus figure being the standard error of the mean of n (16) plots. The coefficient of variation based on the standard deviation of the individual values was 35 per cent.

The 12 plots of one-tenth-acre each yielded 18.3 $\pm$ 2.91 seconds per tree, with a 16 per cent coefficient of variation. A third size plot, one-fortieth acre, was tried by rangefinder but discontinued as too inefficient; two such plots required 51 seconds per tree, on the average.

Fifth acre strips

The long narrow plots, 400 ft. by 21.78 ft., were areal rather than linear sampling units. The strip method was speeded by doing only what was necessary to measure the same things that are measured by the other methods. The procedure was not the same as that of line-strips (Lindsey 1955), since crown cover was disregarded and the "C" figures of the line-strip were not recorded. Those trees not obviously in or out of the strip are checked by twice laying down a 65.34-inch rod perpendicularly from tape to tree center.

Two 200 ft. steel tapes were fastened together so that numbers read in the same direction for both. Before starting the timing, the 200 ft. length wound on a reel (from the high end) has been carried from the previous site on the reel, the other (projecting) 200 ft. length has been dragged lengthwise. The recorder has walked with the drag man until a starting point for the new strip is reached; the starting time is now taken and the recorder waits at the starting place alone until the zero end of the dragging tape comes along. He secures the zero end thong by a short brittle dead stick (breakable later by a strong pull from the far end) thrust into the ground. Thus dragging time for the entire 400 ft. length is included in timing operations at, rather than between, units.

The drag man continues from the 200 ft. to the 400 ft. site, unreeling the rest of the tape as he goes, and at 400 ft. he stretches and secures the far end. He walks directly back along the tape

to join the recorder, who has begun to work up along the tape, measuring diameters of included individuals and recording data. For the remainder (most) of the strip length, the drag man determines which trees are included, calls their names and measures and calls their diameters to the recorder. The latter watches for each 50-foot interval (made conspicuous by colored adhesive tape) on the steel tape, and, at each, draws a line across the field record sheet to separate tree data by fortieth-acre strip-quadrats. From these, or from twentieth-acre (100 ft.) or tenth-acre (200 ft.) fractions or the full fifth-acre strip (400 ft.), an appropriate quadrat size for expressing frequency can be selected later. Finally, from the 400 ft. end, a pull loosens the other end, and the recorder pulls the tape in hand over hand while the other reels up the slack tape to the bulky junction at 200 ft. The finish time is taken when this is done; and all is ready for dragging to the next sampling site.

Ten strips of fifth-acre area were timed; the average time per tree was 23.8 ± 1.38 seconds, and the coefficient of variation 18 per cent.

Point-centered quarter method

Like the random pairs method, this is a distance or spacing method (Cottam, Curtis, and Hale 1953; Cottam and Curtis 1956). The procedure used was kindly suggested by Dr. Grant Cottam (personal communication, 1956) as the most efficient for this method. A rangefinder is faster than a tape for measuring point-to-tree distances, and was used. The point man, who has done the pacing from the previous point, establishes a new point by a Jacob's staff or stake thrust vertically in the ground, and uses its shadow to determine the four quarters about the point. The other man, carrying the clip-board, tapes and writes down the species and diameter (or basal area directly) of the tree nearest the point in each of the back quarters. The point man then recites to the recorder the distances he has already measured by the range-finder. Each man measures diameter of one of the two front trees, and the recorder writes down the data. If the point man gets all four distances measured while the recorder is taping the two back trees, the point man will tape both front trees.

Using 38 points (152 trees) for time trials, 22.8 ± 1.04 seconds per tree was obtained. The coefficient of variation was 28 per cent.

Full Bitterlich method

The Bitterlich variable plot-radius method when used for both density and basal area is herein termed the "full Bitterlich method" to distinguish it from a combination method described below that utilizes the Bitterlich principle for basal area only. In practice the full Bitterlich method is a point method. Its theory has been explained in several papers (Bitterlich 1947, 1948; Grosenbaugh 1952, 1952a). Basal area per acre for a given species (B_2) is computed by the formula $10\ N_p/n_p$, where N_p is the number of individuals of the species at all sampling points and n_p is the number of points. Density per acre for a given species (D_2) is the sum of all the D_5 figures for the different size classes. The D_5 figure is $(N_{pc})\ k/n_p$, where N_{pc} is the number of individuals of a species in a given size class at all points, and k is 10 divided by the basal area (in sq. ft.) of a stem having the median diameter (in inches) of the size class being considered (Lindsey 1956). Initial tabulation of the various possible k values simplifies the computation of D_5.

The angle gage rather than the prism was used to give a 104.18′ angle, with a basal area factor of 10. (A large nail was set in the end of the gage beyond the front sight and filed to a point, enabling one to stick the gage upright in the ground within reach, until needed; the gage was used also as the point stake for the quarter method). The point man turns through a full circle, calling each accepted tree and the midpoint (in inches) of the diameter class in which he estimates it to be. Four-inch size classes were used.

Fifty-one timed Bitterlich points yielded the second best time per tree of all the methods, 12.1 ± 0.473 seconds, with a CV of 28 per cent.

Since density determinations by this method are based on visual estimates of size class rather than on diameter tape measurements, the question of the accuracy of such estimates is of interest. The larger a tree, the less accurate are the visual estimates of diameter, and this deciduous forest contains many large and very large trees. Twenty untimed Bitterlich points were run, in which visual estimates of size classes were recorded, but later checked by diameter tape. Of the 200 trees tallied, 24 were placed in the wrong size class, but always an adjacent class. Ten of these were white oak; the fact that these and nearly all wrongly guessed individuals of other species were large trees did not affect the accuracy of the basal area results, since the size class estimation is used for density, not basal area. The per acre density result for white oak, based on the original size-class estimates, differed by only 0.62 per cent from the density computed from the diameter tape measurements.

Bitterlich combined with circular plots

The standard Bitterlich method could be made more accurate for density by taping rather than estimating diameters, but this would nullify its speed advantage. Density computations in the laboratory are roundabout and time-consuming, a disadvantage not reflected in the field time results.

A newly published combination of the quadrat and Bitterlich methods (Lindsey 1956) was timed at 50 points. The point man rotates through 360° with the Bitterlich gage, calling to the recorder merely species names of accepted trees. Still at the same point, he looks around the circle again without using the gage, calling tree names and estimated 4 in. size classes for only those stems within 37.2 ft. of the point. When a stem cannot be judged with certainty as in or out by the unaided eye, it is sighted through the six-inch-base rangefinder. The second rotation at the point thus determines density and frequency (by size classes as well as species) for a 0.1 acre circular plot.

Since the Bitterlich method is used only for basal area, the estimation and recording of tree diameters during the first rotation are omitted. It took 4.6 ± 0.18 second per tree (*CV*, 26.5 per cent) with the angle gage for finding basal area only. The final computation involves only multiplying by 10 the average number of individuals of a species per point.

The tenth-acre circle plots require only 4.4 seconds per tree, since taping for diameter is omitted. Later computation for density on a per acre basis is extremely simple. The time per tree for the combination method is 9.0 seconds.

The lower time per tree figure for this method with two rotations at the point than for the full Bitterlich method with one calls for explanation. Since accuracy of density by Bitterlich depends on good size-class estimates, time must be taken to get a good view of the tree and to judge its diameter size class with some care. In the combination method, because nothing else hinges on size estimates, this operation was considerably speeded. The angle gage need not be removed from the eye after each tallied tree, but could be held there throughout the rotation for basal area. No trees outside the tenth-acre plot were involved in size estimation; in the woods studied this meant fewer trees needed for size estimation per point.

Laboratory Procedure and Results

Adequacy analyses from the map

Whereas the actual stand was necessary for timing the methods, the map made possible their accurate and uniform application and avoided inconsistencies of species identification. More important, the map rendered feasible the intense sampling needed for accurate statistical determination of sampling adequacy. The statistical work utilized data from 70 fifth-acre strips, 80 each of fifth-acre, tenth-acre, and fortieth-acre squares, 240 tenth-acre rangefinder circle plots, 166 fortieth-acre circles, 290 full Bitterlich points, 240 combination rangefinder-Bitterlich units, and 160 different points sampled by the quarter method. Individual points on the map were numbered and used for many different methods in such ways that the assemblage of units for each method was distributed over the map in a stratified random manner.

Each figure for expressing the field time for a given method is based on a single designated species only. It is suggested that species used should be important ones in the stand but not the principal one, which in Donaldson's Woods is white oak. Two species were used, separately, for determining percent standard error of sampling as a contribution to field time determination. One was beech, the species ranking first in density (28 per acre) in the complete census, and second for basal area (10.3 ft. per acre). The other was sugar maple, which stood third in density (23.3) and fourth in basal area (6.1 ft., Table I). If lower ranking species had been used for field time computations, the times would have been longer and much less accurate, because of the poorer representation of such species in the stand data.

Our sampling methods except the quarter and

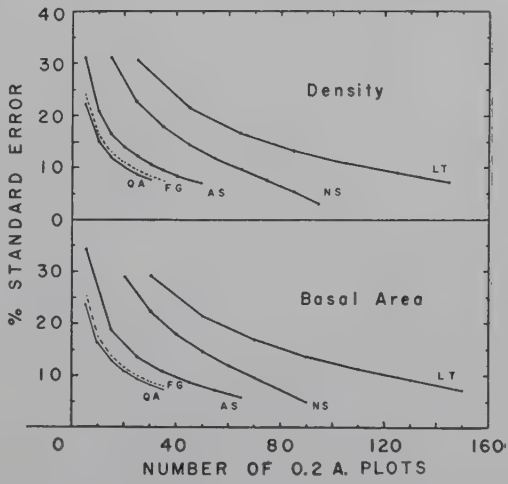

Fig. 3. The relationship between number of fifth-acre square plots and per cent standard error for density and basal area of white oak (Qa), beech (Fg), sugar maple (As), black gum (Ns), and tulip tree (Lt).

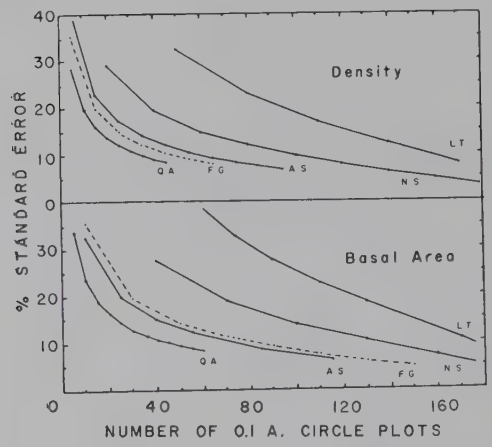

FIG. 4. The relationship between number of tenth-acre circle rangefinder plots and per cent standard error for density and basal area of white oak (Qa), sugar maple (As), beech (Fg), black gum (Ns), and tulip tree (Lt).

TABLE II. Comparison of methods for sampling the density (D) and the basal area (B) of sugar maple at the sampling intensity required for 15 per cent standard error. (See text for exact field procedures)

Method		No. units required	No. stems required	Time per stem, seconds	Time at units, hours	Inter-unit time, hours*	Field time, hours*	Rank of method*
0.2-acre square	D	18.2	448	31.8	3.96	....	....	..
	B	22.3	549	31.8	4.85	0.32	5.17	6
0.2-acre strip	D	17.0	419	23.8	2.77	....	....	..
	B	18.7	460	23.8	3.04	.24	3.28	3
0.1-acre square	D	29.0	357	41.5	4.12	....	....	..
	B	37.9	466	41.5	5.38	.43	5.81	7
0.1-acre circle	D	32.4	399	18.3	2.03	....	....	..
	B	40.0	493	18.3	2.51	.46	2.97	2
0.025-acre square	D	74.0	228	76.7	4.85	....	....	..
	B	136.0	419	76.7	8.93	.91	9.84	9
0.025-acre circle	D	74.0†	228†	51.0	3.22	....	....	..
	B	136.0†	419†	51.0	5.94	.91	6.85	8
Quarter	D	66.0	264	22.8	1.67	....	....	..
	B	104.4	418	22.8	2.64	.76	3.40	4
Full Bitterlich	D	87.0	888	12.1	2.99	.67	3.66	5
	B	59.3	606	12.1	2.04	.. ..	...	..
Rangefinder-Bitterlich	D	32.4	399	9.0	1.00	....	....	..
	B	59.3	606	9.0	1.51	.54	2.04	1

*Last 3 columns based on the attribute (usually B) sampled less efficiently; last column numbers the methods in decreasing order of efficiency.

†No fortieth-acre circles were sampled by map. It seems logical that the number of circles and squares should be equal for any standard error; therefore, the number of fortieth-acre units for circles is copied from the number of squares. The differences in numbers of 0.1-acre squares and circles is probably due to sampling variation.

the Bitterlich are areal. For each of the areal methods, the per cent standard error was computed for several sample sizes (numbers of units). The sample size is designated by n. The n values were chosen so that the per cent standard errors would range from about 8 to about 30. The relations of the standard error to n are graphed in Figures 3 to 6 for 3 plot sizes and for 5 species. The number of units for 15 per cent standard error is called r. From the graphs or by computed interpolation, the r values were determined for each size of plot and for each species.

TABLE III. Comparison of methods for sampling the density (D) and the basal area (B) of beech at the sampling intensity required for 15 per cent standard error. (See text for exact field procedures.)

Method		No. units required	No. stems required	Time per stem, seconds	Time at units, hours	Inter-unit time, hours*	Field time, hours*	Rank of method*
0.2-acre square	D	12.2	300	31.8	2.65	....	....	..
	B	13.5	332	31.8	2.94	0.30	3.24	3
0.2-acre strip	D	9.5	233	23.8	1.54	....	....	..
	B	20.9	514	23.8	3.40	.25	3.65	5
0.1-acre square	D	23.5	230	41.5	3.34	....	....	..
	B	30.0	370	41.5	4.26	.39	4.65	8
0.1-acre circle	D	25.0	308	18.3	1.56	....	....	..
	B	47.0	579	18.3	2.94	.47	3.41	4
0.025-acre square	D	45.9	141	76.7	3.01	....	.	
	B	83.4	257	76.7	5.47	.65	6.12	9
0.025-acre circle	D	45.9†	141†	51.0	2.00	....	....	..
	B	83.4†	257†	51.0	3.64	.65	4.29	6
Quarter	D	55.4	222	22.8	1.40	....	....	..
	B	136.0	544	22.8	3.44	.91	4.36	7
Full Bitterlich	D	67.6	691	12.1	2.32	.58	2.90	2
	B	54.2	553	12.1	1.86		..	.
Rangefinder Bitterlich	D	25.0	308	9.0	0 77	....	....	..
	B	54.2	553	9.0	1.38	.50	1.88	1

*Last 3 columns based on the attribute (usually B) sampled less efficiently; last column numbers the methods in decreasing order of efficiency.

†No fortieth-acre circles were sampled by map. It seems logical that the number of circles and squares should be equal for any standard error; therefore, the number of fortieth-acre units for circles is copied from the number of squares. The differences in numbers of 0.1-acre squares and circles is probably due to sampling variation.

All r values in Figures 3 to 6 and in Tables II and III are for the finite population, which is the 20.145 acres of Donaldson's woods. For an infinite population, r values would be somewhat greater. Any population can be considered infinite if the total area of the sample plots is less than about 5 per cent of the area of the woods (population).

The variance is the square of the standard deviation or of the standard error. Now let—

$\bar{x}$ = the average of the character being estimated,

s^2 = the variance of the individual sample units,

$s^2_{\bar{x}}$ = the variance of the average,

p = the standard error as a decimal fraction of the average (the per cent standard error divided by 100),

n = the number of sample units in the sample, and

N = the number of sample units required to cover the entire population (woods) with no overlapping.

Now, for an infinite population, $s^2_{\bar{x}} = s^2/n$. For a finite population, $s^2_{\bar{x}} = [s^2/n]\ [(N-n)/N]$. In other words, the variance of the average is that for an infinite population multiplied by the fraction of the total population area which is not in the units sampled. If the entire area of the population is in the "sample," we have a census; and the average is free from error—provided no mistakes were made in taking the data.

For a finite population and a standard error of the average as a specified per cent of the average

$$(p\bar{x})^2 = [s^2/n]\ [(N-n)/N].$$

For a 15 per cent standard error this becomes

$$(0.15\,\bar{x})^2 = [s^2/n]\ [(N-n)/N].$$

This cannot be solved directly for n. Therefore, 2 or more values of n are used; the per cent standard error is computed for each; and from a curve such as those in Figures 3 to 6, or by computed interpolation, the n for 15 per cent standard error is determined.

Because of the general meaning of a standard error, if we achieve a 15 per cent standard error in each of many sampling investigations we expect 67 per cent of our estimates of density, basal area, etc., to be within 15 per cent of the true value; and we expect 33 per cent of our estimates to be more than 15 per cent away from the true value.

For the Bitterlich method, the r value for basal area for an infinite population was computed in the ordinary simple manner. For density the r value was computed by a tedious procedure which we do not describe here.

The standard error—and consequently the r value—cannot be computed easily for the quarter method for all species nor for any individual species. Our computations were made thus: From the data for the 160 sampling points we drew 40 stratified random samples of 20 points each and computed 40 averages for all species and for each species. We then computed the variance of these 40 averages. Averages from samples of this size were nearly normally distributed. Then we computed n for 15 per cent standard error from $s^2_{\bar{x}} = s^2/n$. In this $s^2_{\bar{x}}$ is the desired standard error $= (p\bar{x})^2 = (0.15\,\bar{x})^2$, s^2 is the variance of the 40 averages from 20 points each, and n is the number of 20-point samples needed to attain 15 per cent standard error. Multiplying n by 20 gave the number of points at which measurements must be taken in an infinite population. A similar procedure was used to obtain 40 averages from 32 points each and an estimate of how many points were needed for a 15 per cent standard error. The necessary numbers of points entered in Tables II and III are averages of the values from samples from 20 and from 32 points. The 40 samples of 20 incorporated each of the 160 points exactly 5 times; and the 40 samples of 32 used each of the 160 points exactly 8 times.

No definite areas are in the quarter and the Bitterlich samples. Therefore, the required number of sample points for an infinite population could not be adjusted to the number for a finite population by the formula used for areal samples. An example will show clearly how the adjustment was made. Suppose that by the Bitterlich or by the quarter method 79 points were needed for an infinite population. By some areal method in which 79 units also were needed for an infinite population, 74 units were needed for the finite population. Therefore, for the Bitterlich or the quarter method, 74 points were used as the number needed for the finite population when 79 were needed for an infinite population.

In actual sampling of a stand by the Bitterlich or by the quarter method, the adjustment to a finite population could not be made. One would compute the needed number of points for an infinite population; then if the sampling was intensive, one could feel that the true precision was somewhat better than that computed. In actual sampling by either of these 2 methods, few persons would bother to compute the precision of the average density from the Bitterlich method or the precision of either the average density or the average basal area for the quarter method. This is true because the computations are tedious.

Non-areal methods.—Tables II and III show that the full Bitterlich method required more units and trees than the combination method, but fewer units than the quarter method. However, the latter required considerably fewer trees than either of the other two. The largest number of stems is required by the full Bitterlich method, because of its poor sampling for density. All other methods sample density better than basal area; hence, the basal area results are limiting or definitive, except in the Bitterlich method.

Areal methods.—Basal area data from areal sampling did not yield any generalization as to whether small plots or large plots require more total stems.

Three species in addition to beech and sugar maple were used—white oak, black gum, and tulip tree, which ranked second, sixth, and twelfth in density, respectively, among the 22 species in the

stand (Table I). Curves for the 5 species (Figs. 3-6) bring out the relationship between number of units and per cent standard error, for each combination of quadrat size and type tested.

Fifteen per cent standard error has been selected arbitrarily as a standard for comparison of methods; it is not our purpose here to recommend that any particular adequacy level be adopted. It is generally impracticable in general sampling operations to achieve a desirably low standard error for any species except a very few important ones; in a detailed study the ecologist must compromise between the number of units desirable and the number that are feasible. For example, Figure 3 shows that it took 18 of even the largest square or circle plots, 0.2 acre, to give a standard error as low as 15 per cent for density of sugar maple, the third commonest species. Nearly double that number of units was required to reduce the error to 10 per cent. The curves show that fewer sampling units, hence fewer trees, are required to sample white oak than beech, even though the latter is the more numerous. This is explained by the more nearly uniform dispersal of the oak.

Obviously, if a curve had been plotted for all species lumped together, it would have indicated a much lower per cent standard error than that of any single species, for any given number of plots. However, the variability of the total stand figure is not a satisfactory basis for judging adequacy of sampling.

The fortieth (0.025) acre or 10 x 10 meter plot, the size most used by forest ecologists to date, yielded the results plotted in Figures 5 and 6. For sugar maple, 136 such units are required in Donaldson's Woods, many more than generally used in a 20 acre stand, to sample so that neither its density nor basal area exceeds 15 per cent error; 83 plots would be needed to sample the most abundant species (beech) this well. Since with fifteen per cent standard error, 33 per cent of many averages are expected to be more than 15

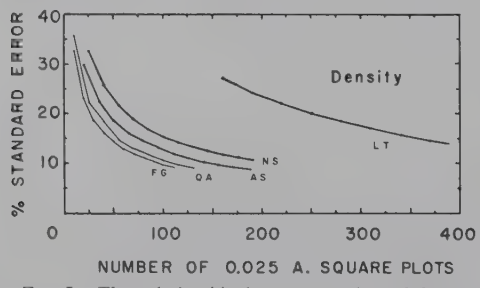

FIG. 5. The relationship between number of fortieth-acre square plots and per cent standard error for density of beech (Fg), white oak (Qa), sugar maple (As), black gum (Ns), and tulip tree (Lt).

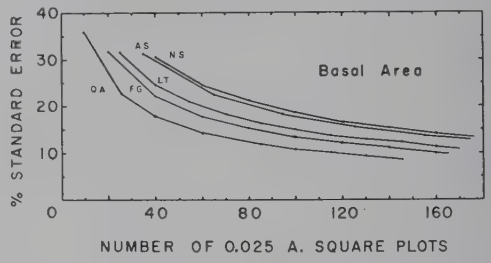

FIG. 6. The relationship between number of fortieth-acre square plots and per cent standard error for basal area of white oak (Qa), beech (Fg), tulip tree (Lt), sugar maple (As), and black gum (Ns).

per cent of the average from the true average density or basal area, the confidence derived from even 136 fortieth-acre quadrats leaves something to be desired. For species less numerous than sugar maple, many more plots would be necessary to maintain this 15 per cent adequacy level. There are actually 2.0 tulip trees per acre, and it would require 360 of these fortieth-acre plots, totalling 9 acres, to sample this species with 15 per cent error (Fig. 5). For a worker interested in tulip tree alone, a full count of the 20-acre stand would be faster and much more reliable than running 360 small quadrats. By use of the largest square plot studied (0.2 acre), it would take 81 plots (16 acres) for 15 per cent error for tulip tree (Fig. 3). Only field time determinations based on one or more important species, taking into consideration the time needed to lay out various size plots, their relative sampling adequacy, and the total walking time between the required number of units, can furnish dependable general guidance for selection of a sampling method.

Time at units

The number of stems required for the adequacy standard, multiplied by the average time per stem gives an important criterion of each method, namely, the working time at units. This is shown in the center column of Tables II and III. For readers who cannot agree with our interpretation of the importance of time spent in walking from unit to unit (see subsequent section), it is suggested that "time at units" instead of total "field time" may be considered the basis of comparison between methods. However, use of this as the final criterion is especially unfair to the strip method, in which most of the walking is done within the units instead of between them as in other methods.

On the time-at-units basis, the methods may be rated by requiring that (in the usual sampling of all species encountered) *both* maple and beech be sampled at least as well as 15 per cent standard

error. The decreasing order of speed is as follows—combination method (1.51 hr.), tenth-acre circle (2.94 hr.), full Bitterlich (2.99 hr.), fifth-acre strip (3.40 hr.), quarter method (3.44 hr.), fifth-acre square (4.85 hr.), tenth-acre square (5.38 hr.), fortieth-acre circle (5.94 hr.), and fortieth-acre square (8.93 hr.).

A test was made of the randomness of distribution of trees of all 22 species together and of the trees of each of 6 individual species separately. To do this, as much as possible of the area of the woods was divided into strata 200 ft. square. Then each stratum was divided into sixteen 50-ft.-square quadrats. The variation among strata was compared with the variation within strata by an *F* test. All trees together and each one of the six species taken separately departed significantly from a random distribution.

When the stand was divided into four areas of approximately 5 acres each, the number of trees irrespective of species showed a highly significant departure from homogeneity by a Chi-square test. However, Cain (1932), Braun (1950) and J. E. Potzger (personal communication 1953) considered Donaldson's Woods a "stand." The quarter method is better suited to a more nearly homogenous stand in which the separate species are randomly dispersed. This method ranked third (in speed of work within units) for maple (2.6 hr.), and sixth for beech (3.4 hr.). The beech showed a greater tendency to aggregated dispersal.

To equal the combination method in time-at-units, the quarter method time would have to be reduced from our 22.8 seconds per stem to 13.0 seconds per stem for meeting the adequacy standard for maple and to 9.1 seconds for beech. The latter time would mean only 36 seconds at the point for the entire procedure on the tree stratum. The necessity of going to each tree for trunk measurement imposes a practical limit on the speed per tree. The fact that only 4 trees are tallied per unit necessitates a fairly large number of points. However, the number of stems required (maple, 418; beech, 544) is fewer than for some other methods.

The full Bitterlich method and the combination method require more trees for adequacy than do other methods. Especially high is the required stem number for density by the full Bitterlich method. Despite this, the combination method rates first and the Bitterlich method third in working speed at units, because they take far less time per tree than other methods.

Inter-unit time

The aggregate time it takes for the circuit through the stand, exclusive of the time spent sampling at the points or plots, may be called the inter-unit time. This time cannot properly be disregarded in a study of field efficiency, since inter-unit time is not proportional to time within sampling units, but to the number of units needed to get the selected adequacy level. For a given method, the sum of time at units and inter-unit time is "field time." The latter measures the entire efficiency of the method except office computation. The shorter the field time, the more efficient the method is in the field.

An index map of the stand was prepared showing the exact locations of all points sampled from the large-scale map sections. Selecting from these points to produce a stratified random pattern, the maximum number of units (136) required by any method for obtaining not higher than 15 per cent standard error, for *either* basal area or density of sugar maple, was marked on the index map. The shortest circuit for visiting all 136 points was found to be a very zig-zag course up one side of the area, across the top, down the other side, and across the bottom. A scale marked in feet was used to determine the inter-unit distances. The next smaller number of points is required by the quarter method, so 104 of the same 136 points, maintaining a stratified random distribution on the map, were used. The shortest trip to visit all these points was measured off. By such continual elimination, each method requiring successively fewer points utilized some but not all of these points used for the previous method. The total distance of the circuit became progressively less as fewer points were required, but the units for all methods were distributed in a stratified random way.

This entire operation was repeated on another index map, based on a different stratified random arrangement of an initial 136 points.

For each method, the average of the two trials was used, converted to time. A reasonable rate of walking with equipment from unit to unit had been timed in the woods as 0.00008325 hr. per foot. Circuit distances were converted to time in hours, and time in hours was plotted against the number of units needed for sugar maple (Fig. 7).

The straight line in this Figure, determined by the points plotted for sugar maple, was used to find the inter-unit times for beech, based on the number of units previously found necessary for standard error not higher than 15 per cent for *both* density and basal area for beech. This procedure was proper because only the number of

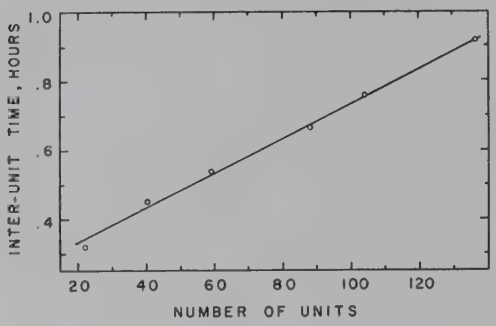

FIG. 7. Each circle shows the total walking time to make the circuit of the number of (stratified-random) units required in a given sampling method to obtain 15 per cent standard error for sugar maple. The time spent in sampling work at the units is not included. The smoothed curve based on data for sugar maple forms the straight line, which facilitates determination of the inter-unit times for the different numbers of units required in these methods for species other than sugar maple.

needed units (for adequacy) varied from species to species, and it was this number, rather than the operation at the unit, which determined the inter-unit distance and hence inter-unit time. Consequently, the curve on a graph derived from one species could be used for finding the inter-unit time for any other species for which the number of units was known.

Any method requiring 136 units, as did the fortieth-acre quadrat for maple and the quarter method for beech, necessitated walking 10,953 ft. from unit to unit, which took 0.9 hour. Forty tenth-acre rangefinder circles required 0.46 hours inter-unit time, while 19 strips called for only 0.24 hours travel between strip-ends. Time spent working along the strip was of course included in the time-within-units category. Thus, inter-unit time for one method was almost four times that for others.

The relationship of the number of trees and the time per tree differs among the methods. The slowest methods were the small plots, especially the squares; while the required number of trees was lower than in most other methods, the high time requirement per plot (and per tree) gave rise to an excessive time-at-units figure. Tables II and III reveal that work within units took about twice as long for the smallest squares as for fifth-acre squares.

Field time

The total field time for a method, including the inter-unit time, is the final measure of field efficiency (Tables II and III). The shortest time, or highest efficiency, was found for the combination rangefinder-Bitterlich method. Its field time was approximately two-thirds that of the next two fastest, the full Bitterlich method and the tenth-acre circle. Following these two, the order differs somewhat between maple and beech, but the areal rangefinder plots (circles) excel the squares, and the larger plots excel the smaller ones of the same shape.

In increasing order of field time required so that neither maple nor beech have higher than 15 percent standard error by a given method, the methods rank as follows—combination method (2.04 hr.), tenth-acre circle (3.41 hr.), fifth acre strip (3.65 hr.), full Bitterlich (3.66 hr.), quarter (4.36 hr.), fifth-acre square (5.17 hr.), tenth-acre square (5.81 hr.), fortieth-acre circle (6.85 hr.), and fortieth-acre square (9.84 hr.).

A ranking based on averages of field times for beech and maple for each method differs only in the reversed position of the strip and full Bitterlich methods.

DISCUSSION

Areal methods

The areal methods tested in this study include conventional (surveyed) square plots, circular plots determined by rangefinder, and strips. Areal methods are unbiased, relatively simple in underlying theory, and the computations involved are straightforward and often extremely simple. All the areal methods proved more efficient for density than for basal area.

Conventional quadrats.—Laying out plot boundaries by tapes, cord, etc., so obviously limits field efficiency that intensive time trials were not made for such procedures. Even by the more rapid "diagonal method" in which only the corners are marked, the high field times showed that the square plot method is inferior.

Current opinion among ecologists seems to favor smaller plots over larger ones. The summarizing figures for order of field efficiencies (see Field time, above) ran directly counter to this view. For both diagonally-surveyed squares and rangefinder circle plots, efficiency varied directly with size, within the limits of plot size investigated. This was not merely because of the longer total walking time between the many smaller plots, but was also due to the high investment of time per tree at the unit.

Both species indicated that, for both square and circular areal plots, the fortieth-acre size is distinctly the worst of all 9 methods tested, whether based on time at units or field efficiency as a whole. It took from 3.3 to 5.9 times as long as the fastest method to get the same results. One-fortieth-acre is practically the same area as the 10 x 10 meter quadrat, which for a long time was almost a

standard sampling unit among forest ecologists in this country. In contrast, foresters have generally preferred much larger plots.

The diameter tape, or another device for obtaining basal area directly or ultimately, must be used for each individual trunk; this tends to lower efficiency in comparison with methods using the Bitterlich principle for the basal area component.

Rangefinder circle plots.—This method is far superior to square plots of the same size. Its speed is due largely to the fact that most trees can be readily seen to be inside or outside the tenth-acre plot by unaided visual estimation; only trunks near the imaginary boundary need to be sighted through the 6-inch-base rangefinder. However, the necessity of measuring each tree by diameter tape tends to reduce its efficiency. The method is unbiased provided that no bias exists in the way the distance to questionable stems is measured. To avoid such bias, the instrument must be correctly adjusted and properly used. The recommended 0.1-acre size simplifies computations of density and basal area.

With all methods involving the rangefinder, reasonably good light and weather are required and very dense obscuring undergrowth proves a nuisance. Working with 0.2-acre plots is not practicable by rangefinder, because accuracy of the instrument drops off rapidly at distances beyond the 37.2 ft. radius of the 0.1-acre plot.

Strips.—The strip is an elongated areal sampling unit. The 0.2-acre strip, 400 ft. long, was used. This unit yields data comparable with data from the other methods tested.

The line-strip (Lindsey 1955) yields cover in addition to density, basal area, and frequency. Since the cover parameter is not obtainable by the methods tested herein, the line-strip method is not comparable to them and has not been included. The time required to measure cover interception on the line would probably give the line-strip method a considerably lower field efficiency than any method except square quadrats, unless one attempted to weight the evaluation to credit the valuable coverage parameter.

To be tallied a tree center can be only 10.9 ft. away from the tape; the short distance is easy to estimate accurately. Since only borderline trees need be actually checked by extending the rod toward them, the method stands third in efficiency. This short lateral distance (the half-width of the plot) confers another advantage. Dense undergrowth causes far less trouble than in other methods by obstructing vision. This is especially so in comparison with methods that involve full operation from the point. The strip method is ideal for an operator having poor eyesight or when the weather or light conditions make visibility poor.

A benefit of length is that most of the strip area is not in sight when the starting point and direction of the strip are determined. This contributes a random tendency so that elaborate randomization is less necessary in placing strips than for other methods.

The cost of two 200 ft. steel tapes is a point against the method for the casual user. One tape could be moved forward for the second 200 ft., but two fastened together are preferable.

The quarter method

The rangefinder used in the quarter and two of the other methods is considerably less expensive than the long steel tapes used in strip sampling, and is easier to carry. The point-centered quarter method is fairly efficient although it is less rapid than usually considered, if compared with other rapid methods for a given level of sampling adequacy. By using only four trees at a point, the data are unlikely to be influenced unduly by an atypical spot in the woods, if enough points are put down. On the other hand, most of the potential information about the trees near each point is disregarded, because of the four-tree limit. By all other methods (except quadrats yielding four trees each or fewer) the spots visited are more fully exploited so that not nearly so many of them are needed. The total number of trees required is less than by several other methods, but with only four trees per point the number of points needed is still very high.

Unlike methods using rangefinder plots, the quarter method requires sighting the instrument on every tallied tree, causing some loss in efficiency. Because trunk size is measured by tape, complete operation from the point is not possible, as it is in the full Bitterlich method and in the combination method. Office computations of vegetational attributes by the quarter method are indirect and laborious.

This method is perfectly unbiased only when the trees are randomly dispersed. As stated by Cottam and Curtis (1956), "Aggregation tends to increase distances obtained with the closest individual, random pairs, and quarter methods. . . ." This results in underestimates of density and basal area. However, since the method has given good results for a number of workers, its bias for species tending toward a clumped dispersal may not be very important in practice. Probably more serious is the difficulty previously mentioned of computing a measure of the precision of estimates.

Despite the speed of quarter sampling at the point, this method ranked fifth in field efficiency

among the methods tested. Merely walking the circuit of the 136 points required for beech by the quarter method, without stopping at any of the points for sampling, takes about half as long (0.91 hr.) as the sampling plus total inter-unit walking time (1.88 hr.) by the combination method.

Obviously, the practicing ecologist would seldom if ever use 100 or more points in quarter-method sampling, any more than he would use the large numbers of small quadrats indicated earlier as needed for 15 per cent standard error. But, without doing so, one could not, except rarely by chance, achieve sampling adequacy in Donaldson's Woods nearly as good as this. It is necessary to use these high numbers of units to attain this level of sampling adequacy and to give comparability with the other methods in the present study; and when many units are used, stratified random placement insures their wide scattering with the resulting high inter-unit time value.

Whereas sampling efficiency is always desirable, the level of sampling adequacy to be sought will depend on the objective of the work. When attention is focused on one or a few stands, a low standard error may be demanded. On the other hand, in studies of a vegetational continuum (e.g., Brown and Curtis 1952), very many stands are sampled and there is little stress on the characteristics of any particular stand. Values for a given species in the stands are plotted to yield a curve for that species. Since a drastic smoothing of each curve is carried out, the precise value for each stand is not critical. The quarter method has usually been used for collecting data for this type of analysis, where insistence on high sampling adequacy would slow up the work without commensurate gain. However, one of those sampling methods that appear to be more efficient than the quarter method could be applied, to permit getting data at the same adequacy level in less time.

Full Bitterlich method

When used for both basal area and density the Bitterlich method has well-known advantages, but suffers from some striking weaknesses. It is unbiased provided that (1) the instrument used is properly matched to the eye of the operator and (2) the operator has no bias, toward either too large or too small diameters, in guessing the tree size classes needed for density computations. An angle gage can be improvised or a wedge prism can be bought cheaply, and both are easily portable, especially the prism.

Complete operation from the point is afforded, eliminating the need for a diameter tape. Avoiding the direct measurement of trunks permits great speed per point and per tree, but the large number of points needed for density by this method tends to counteract that advantage. If basal area and not density is desired, as may be the case in forestry, this part of the method used alone is extremely rapid and efficient in both field work and computation.

Although not biased for density, the Bitterlich method is so inferior for it that many more points and trees are needed than for basal area. There are several reasons for this. Diameters of all tallied trees must be guessed and recorded by size classes. At equal distance from the observer, the larger the tree the harder it is to estimate visually its correct size class. On the other hand, a given tree size is made more and more difficult to estimate for diameter as its distance from the point increases. Both these factors of difficulty work against Bitterlich density results, for it is characteristic of this method that the larger a trunk is, the farther from the point it can stand and still be tallied. A four-foot trunk would be tallied at 132 feet, and at this distance in the woods its size class estimate is subject to considerable error. Small trees must be close to the point to be tallied. These are easy to judge because they are both small and near, but the method tallies very few small trees in proportion to their number in the stand or to the number of large trees tallied.

It is possible that a worker might consistently overestimate or underestimate trunk diameters; this would bias his density data but would not affect the basal area results.

Good weather, good visibility, and sparsity of obscuring undergrowth are particularly desirable for the Bitterlich method, because both density and basal area depend on the view from the point itself. This becomes more important when large trees are numerous relative to small ones.

It is not possible to obtain frequency or relative frequency by the full Bitterlich method. Since this attribute was not studied, the present comparison is unaffected. But since all other methods that were included yield at least *relative* frequency, opinions on the seriousness of this disadvantage will vary with the workers' interest in frequency. Another flaw in the method is the extreme difficulty previously mentioned of computing the standard error for density.

Field efficiency is not the final criterion in the evaluation of sampling methods. Density calculations by the Bitterlich method are roundabout and laborious. In any method with high demands for office computation time, like the Bitterlich and quarter methods, efficiency gained in the field is lost, to some extent, in the office. Because it is difficult to judge the relative value of field time versus office time, only an analysis of field effi-

ciency was attempted. However, it is quite obvious that computation time for basal area is lowest in the Bitterlich method, and that density can be computed in the shortest time for tenth-acre quadrats.

Combination rangefinder-Bitterlich method

This combination method was suggested by several points in the above discussions of the rangefinder circle plot method and the full Bitterlich method. No basic method was superior to all others for both density and basal area, but a combination of the best basic method for density with the best one for basal area seemed to be so.

The tenth-acre circle had excellent field and total efficiency for density, but, like all other methods, was inferior to the Bitterlich method for basal area. The combination method utilized the advantages of both its parent methods, but their disadvantages were largely avoided by using each basic method only for that which it does best. Freed of the retarding effect of a weak partner, each component is improved in time-at-units and field time. Of the methods studied, the combination method ranks first in field efficiency, and, because the office computations for density and basal area are reduced to extreme simplicity, it must be outstanding in over-all efficiency.

Complete operation from the point makes the diameter tape unnecessary. The required instruments, the angle gage, or prism, and the six-inch base rangefinder are rather inexpensive, easily portable, and rapid and convenient to use. Absolute (per acre) data, as well as relative comparisons among species, are obtained; the possibility, found in the full Bitterlich method, of biasing density results due to the worker's own bias in visually estimating trunk diameters is eliminated. Accuracy of density figures does not depend on guessing size classes of distant large trees as in the Bitterlich method, since species density, basal area, and frequency are obtained without any diameter measurements or estimates. If, in addition, it is desired to break down species density by size classes, this is based on the 0.1-acre area surrounding the point. Size estimates are improved, since no trees farther than 37.2 feet away are so estimated, and there is not a disproportionately great number of trees in the poorly judged large size classes. The species density figure (for all size classes of the given species, combined) can be correct even though the size class estimates are inaccurate; this is not true of the Bitterlich method, except accidentally.

Because of its total efficiency, the combination method should be the most suitable sampling method for populations tending toward aggregated dispersal, since, other things being equal, higher intensity of sampling is needed for adequacy than is the case with random populations.

Although all the field work here reported was done by a two-man team, the full Bitterlich method and the combination method are very well adapted to use by one worker equipped with a portable tape recorder. A machine built of magnesium, with its lapel microphone, leather carrying case, and two extra batteries, weigh less than 4 pounds. Another brand on the market is a few ounces heavier. One tape runs an hour, but the machines may be turned on intermittently, when one is actually dictating. Such instruments should find many applications in ecological and other field work.

Summary

A large scale map of an undisturbed 20-acre stand of white oak—beech—sugar maple was sampled intensively by nine forest sampling methods. The number of units and number of trees required for 15 per cent standard error were computed. Each method was timed in the actual stand to determine time per tree. The total number of stems of all species required for 15 per cent standard error for a selected dominant species multiplied by the time per stem gave a total time-at-units figure for each method. To this was added the time required to make the circuit of the required number of sample units; the sum is the field time, the inverse of field-statistical efficiency.

For sampling the density and basal area of *either* sugar maple *or* beech with not more than 15 per cent standard error, the methods ranked in the following order of field time—(1) combination of the rangefinder circle and the Bitterlich method, 2.04 hr.; (2) tenth-acre rangefinder circle, 3.41 hr.; (3) fifth-acre strip, 3.65 hr.; (4) full Bitterlich, 3.66 hr.; (5) quarter method, 4.36 hr.; (6) fifth-acre square, 5.17 hr.; (7) tenth-acre square, 5.81 hr.; (8) fortieth-acre circle, 6.85 hr.; and (9) fortieth-acre square, 9.84 hr.

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THE BEECH FORESTS OF WISCONSIN—THEIR PHYTOSOCIOLOGY AND RELATIONSHIPS TO FORESTS OF THE STATE WITHOUT BEECH[1]

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INTRODUCTION

As a part of the intensive investigation of Wisconsin plant communities being carried out at the University of Wisconsin a study of those woods of the state in which beech (*Fagus grandifolia* Ehrh.) is a component was made. Most of the field work for this research was done during the summers of 1952 and 1953. An earlier paper (Ward 1956) dealt with compositional changes within the beech forests and the nature of the beech border in the state. The present paper is concerned with a third major phase of the study, the general phytosociology of the beech forests and the relationship of these to forests of the state without beech.

Data from fifty-one beech stands distributed over the beech range (Fig. 1) were included in the analysis, and data from eighty-three nonbeech stands studied by previous students at the University of Wisconsin were utilized for comparative purposes.

In selecting beech stands suitable for this study three requisites as to condition were adhered to: the presence of beech; lack of recent general disturbance of any kind; and maturation beyond a pole-tree condition if a second growth stand. Some of the stands were located by reference from

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FIG. 1. The range of beech in Wisconsin and the location of beech stands used in this study.

sources such as county agents, but most were found by driving over secondary roads and investigating any woods that appeared to have possibilities. Approximately four stands were checked out for every one chosen, with cutting, and grazing by dairy cattle the primary causes for rejection.

DESCRIPTION OF THE AREA

Climate

Certain generalizations can be made about the climate of Wisconsin. Consistent with its continental location, winter and summer are distinct seasons. The winters are characteristically rather severe and snowy, particularly in the northern two-thirds of the state, but the more variable southern portion sometimes enjoys milder winters than areas further to the south. In summer the northern portion is dependably cool, whereas the southern portion experiences both times of high temperatures and high humidity, and other periods of pleasant moderation. Over the entire state summer precipitation is notably reliable, although minor droughts occur occasionally in the southern portion.

The frost-free season varies from less than 100 days per year in the extreme northern sections to as much as 175 days in southeastern Wisconsin. Snowfall is heavier in the north, averaging near 55 inches as against 30 inches in the south; total precipitation, however, is usually somewhat greater in the south. Possible sunshine for the state as a whole averages around 50 per cent.

The climatic pattern within the beech forest range, although not sharply distinct from that of other parts of the state, does show certain differences which may be critical in the limitation of beech. Areas to the northwest are on the average noticeably colder in winter, with also a substantial reduction in the length of the growing season. To the southwest of the beech forest area the somewhat higher summer temperatures may result in a significant reduction of effective moisture, the amount of actual precipitation being roughly the same in the beech forest range as in areas immediately adjacent.

Glacial History

The area of the present study was in large part covered with moraine of the Valders stage, the last major advance of the ice sheet in eastern Wisconsin. Some of the most pronounced topographical changes of the region occur in the interlobate moraine formed by deposition between the Green Bay and Lake Michigan Lobes of the Cary advance. Called the "Kettle Moraine" because of deep hollows, it is most strongly developed in the southern portion of the beech range. The later Valders ice advance, in all probability part of an ice sheet from the Labradorian center, was also lobate near its borders, but did not form a pronounced interlobate moraine.

The glacial deposits of eastern Wisconsin contain imported igneous and metamorphic rocks in addition to local limestone, shale and sandstone. The ground moraine which covers nearly all of the eastern part of the state is composed primarily of till, but has areas of stratified sand and gravel. The topography consists of rolling or hilly moraines and till plains, with many areas either covered by lakes or too swampy for agriculture.

Overlying the Cary drift in an area extending northward from Milwaukee and spreading westward across Calumet and Manitowoc counties is a layer of red clay presumed to be the deposit of a lake, or lakes, existent sometime between the Cary and the final Valders advance. Some of this material was ridged up into terminal moraines by the Valders ice. Other lake deposits are present along the shores of Lake Michigan as the result of postglacial enlargements and recessions regulated by changes in drainage of the Great Lakes (Martin 1932).

Soils

The original soil of the beech forest area was derived from the weathering of the bedrock dolomite and sandstone. These residual soils were added to and mixed by the numerous glacial advances. In some areas lake deposits were laid

down over which the glaciers readvanced, working and shifting the lacustrine and previously mixed deposits.

The soils of the beech forest are of two basic groups, gray-brown podzolic over the lower two-thirds of the range, and podzolic in the northern counties. Within these groups several series are represented, the general distribution of which is given by Muckenhirn and Dahlstrand (1947). In the southwestern portion of the beech range where yellowish or grayish-brown loams of the Miami series predominate, the acid surface soils are a loose, friable loam to a depth of about eight inches. The brown subsoil is distinctly heavier in texture, but has a nutlike structure favorable to penetration by water and roots. The Kewaunee soils found along Lake Michigan and extending over the central portion of the beech area are very similar to the Miami, but with a more reddish color and a somewhat heavier subsoil.

Although designated podzols, classical profiles of this group are not abundant in northeastern Wisconsin, primarily because of the highly calcareous parent materials and glacial deposits which tend to inhibit acidic leaching associated with such development. Sandy areas dominated by conifers show greatest evidence of podzolization.

In contrast to the mull humus of the Miami-Kewaunee region, a fairly distinct organic layer of the mor type is usually present in the northeastern Wisconsin beech woods. Underlying this is a layer of grayish-brown silt or fine sand ranging up to about one foot in thickness, and a somewhat heavier subsoil which gives way to a highly calcareous, loose, gravelly, glacial till. Shallow, brownish-gray loam of the Longrie series, deeper clay loams of the Onaway series, and the sandy, low fertility soils of the Vilas series are most important in this portion of the beech range.

Literature Review

Ecological reference of various kinds is made to the beech of Wisconsin in early writings (Lapham 1854, Chamberlain 1877, Roth 1898, Brunken 1900, 1902), but there has not been a general study either descriptive or quantitative of the beech forests of this state. Only two previous studies present quantitative information on the beech forests of the state; Brown and Curtis (1952) included a few stands having beech in their study of the northern hardwoods of the state, and Gilbert and Curtis (1953) present herb data from upland forests of the state, some of which were obtained in stands that have beech.

Perhaps most closely related to the Wisconsin beech forests from a floristic standpoint are similar forests of Michigan. Studies by Quick (1923) and Cain (1935) present data which can be used to show considerable agreement with the woods of the southern part of the Wisconsin beech range. Several species are found in the southern Michigan beech woods which are not found in the Wisconsin woods, including *Liriodendron tulipifera* L., *Nyssa sylvatica* Marsh., *Platanus occidentalis* L., *Quercus bicolor* Willd., and *Sassafras variifolium* (Salisb.) Ktze., but they make up only a small part of the tree population. Data from the northern part of the lower peninsula of Michigan (Quick 1923, Gleason 1924, Wollett and Sigler 1928) indicate a close affinity between the sugar maple-beech-conifer forests of that area and those in northeastern Wisconsin.

Studies in Indiana (Esten 1932, Potzger and Friesner 1943, Jones 1952, and Trotter 1952) provide data which also can be used to show a close relationship between the sugar maple-beech dominated stands of that state and those of this area. Here there are approximately 10 tree species which are not to be found in the Wisconsin woods, but for the most part they are of secondary importance. Williams (1936), in a biotic study of the Chagrin Reservoir near Cleveland, provides data which with little change could be taken from Wisconsin stands; there is a striking similarity in the tree, shrub, and herb composition. Data from eastern New York (Russell 1955) also indicate a basic similarity between the sugar maple-beech forests of that region and those of Wisconsin.

With regard to the taxonomic status of the beech in Wisconsin Camp had this to say (1953, personal communication):

"In Wisconsin there is no one of the basic biotypes present, rather the beech population in Wisconsin is paced by a series of genes derived from the Red Beech; however, there is ample evidence that genes derived from both the southern White Beech and the northern Gray Beech also are present in greater or less amount." Herbarium specimens annotated by Camp, and minor leaf studies by the author indicate that the variation within the Wisconsin beeches follows no particular geographical pattern, and to the present no ecological correlations have been found.

Methods

To sample the tree population the random pairs method was employed, using a four inch or greater d.b.h. criterion for trees. In most cases forty points were taken in a woods, but in a few areas where no large stands were found, smaller woods were sampled to fill in distributional gaps.

Of the 134 stands involved in this study approximately one-sixth of them were sampled with

less than 40 points, usually 20. An estimated minimum size of the smallest stands would be between five and ten acres. The statistical inadequacy of these small samples is recognized, particularly with regard to the infrequent species, and this fact should be borne in mind by the reader. It is felt, however, that the results can be meaningfully interpreted on the basis of general trends.

To check the homogeneity of the tree population within the individual stands a chi-square test was applied. Where 40 points were taken each sheet of 10 points was used as a unit, and the observed and expected number of trees of the species with the greatest density was tabulated in each of the four units. All stands had values for "P" greater than five per cent, with most of them much higher.

Saplings (1"-4" d.b.h.) were sampled by recording by species the four nearest to the point, or in some instances the number less than four that were within a distance of twenty feet from the point. At alternate points (or at every point where only twenty points were taken) a one-meter square quadrat was laid down to sample the herb, shrub, and seedling populations. Stand presence was noted for all ferns and spermatophytes.

In order to obtain a picture of the changing herb pattern as the growing season progressed, several stands were sampled for early spring herbs in addition to the regular sample taken after the tree leaves had reached full development.

The data were used to compute an importance value (summation of relative values for frequency, density, dominance) for each tree species in a stand, and data from the lower strata were used to compute relative density for saplings, and frequencies for herbs, shrubs, and tree seedlings.

Although the study of the environmental factors was not emphasized, some data were gathered. Soil pits were dug in most stands, and notes on the profile were recorded. Three separated samples of the A_1 horizon were taken in a woods, at places not decidedly wet or dry, and combined into a single sample for laboratory determination of moisture holding capacity, and for chemical analysis.

Using a Weston photometer, light readings were taken in eighteen stands, after the trees had fully leafed out. This was made as objective as possible by pacing an arbitrary constant distance, placing the meter on the ground, and putting the light target immediately above the head while kneeling to read the dial; visual bias was largely eliminated in this way.

Results

In order to analyze the unity of the beech forests and to relate them to the southern upland hardwood and northern conifer-hardwood forests of the state, it was decided to place the individual beech stands into northern and southern categories, using primarily the presence or absence of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and yellow birch (*Betula lutea* Michx.) as the basis. Beech stands having one or both of these species were with one exception considered to be northern; a few stands lacking these were placed in the northern group according to other species. A summary of the two types follows.

Southern Beech Stands

Only sugar maple (*Acer saccharum* Marsh.) had an importance value in all stands with beech. Ostrya (*Ostrya virginiana* (Mill.) K. Koch.) and basswood (*Tilia americana* L.) were sampled in all but one, and white ash (*Fraxinus americana* L.) and red elm (*Ulmus rubra* Muhl.) were found in approximately three stands out of four. The majority of species, however, were sampled in less than half of the stands, with several found in only one or two. The decided superiority of sugar maple and beech is more readily seen in a tabulation of the average importance values for each species in all stands (Table I). Together these

Table I. Tabulation of tree composition of the "southern" beech forests

	Number of stands of occurrence	Average importance value	Maximum importance value
Acer rubrum	1	0.2	3.4
Acer saccharum	17	107.6	234.5
Betula lutea	1	0.2	2.9
Betula papyrifera	3	2.3	25.0
Carya cordiformis	4	0.8	4.4
Carya ovata	4	4.5	39.0
Crataegus spp.	1	0.2	6.0
Fagus grandifolia	17	78.2	161.0
Fraxinus americana	13	11.5	27.7
Fraxinus nigra	4	1.5	13.6
Ostrya virginiana	16	19.3	65.9
Populus grandidentata	2	0.9	8.1
Prunus serotina	8	4.0	13.0
Prunus virginiana	1	0.2	3.4
Quercus alba	7	3.8	20.0
Quercus macrocarpa	2	0.5	5.0
Quercus rubra	9	15.1	78.0
Tilia americana	16	28.8	69.1
Ulmus americana	6	6.2	49.0
Ulmus rubra	12	13.8	95.0

two species make up more than half of the total possible value of 300. Other species show fairly high importance values in certain stands, but the averages for all stands in no case approached that of these two climax species. Basswood, next be-

low beech in importance had an average importance value considerably less than that for beech. Ostrya, although usually found with sugar maple and beech, seldom has a high importance value. White ash and red elm, common constitutents of the southern beech forests of the state, are seldom important. Red oak (*Quercus rubra* L.) is sometimes important in beech stands, but occurs usually as a large tree and is insignificant in the small size classes.

Sapling reproduction consists mostly of sugar maple, beech, and Ostrya, with the former often very abundant. Sugar maple is definitely superior in seedling reproduction. The dominance of sugar maple and beech is further seen in the leaf litter, where leaves of other species are much outnumbered.

In early spring the forest floor is often covered by a few species of herbs which complete much of their life cycle prior to full foliage development of the trees; normally to be found with these are other species which carry over into the summer. Table II lists the average and maximum frequencies in seven stands for several of the most important herb species found in spring. The strictly prevernal species quite often show high frequencies in one or two stands, while being rare in others.

By mid June the appearance of the forest floor is quite different. Such species as *Allium tricoccum* Ait, *Claytonia virginica L.,* and *Erythronium albidum* Nutt. have completed their life cycle, and the per cent cover by herbs is considerably less. Average and maximum frequencies for important herb species found in summer in some of the southern beech stands are given in Table II.

TABLE II. Some of the most important herbs found in representative southern beech stands. The stands sampled in summer were in some cases different from those used in the spring

	Spring		Summer	
	Average frequency	Maximum frequency	Average frequency	Maximum frequency
Allium tricoccum	25.0	80.0		
Carex pensylvanica	18.6	40.0		
Circaea quadrisulcata			24.6	75.0
Claytonia virginica	23.6	100.0		
Erythronium albidum	11.4	80.0		
Galium aparine			30.0	100.0
Galium concinnum	16.4	50.0		
Geranium maculatum	22.8	45.0	17.5	45.0
Hepatica acutiloba	20.7	85.0	28.3	60.0
Hepatica americana	13.6	80.0		
Osmorhiza claytoni	16.4	50.0	37.5	80.0
Podophyllum peltatum	22.8	45.0		
Polygonatum pubescens	36.4	65.0	30.8	60.0
Sanguinaria canaaensis	15.7	50.0	30.4	70.0
Smilacina racemosa			17.5	45.0
Trillium grandiflorum	36.4	65.0	18.7	60.0
Viola cucullata			16.7	50.0

TABLE III. Tabulation of tree composition of the "northern" beech forests

	Number of stands of occurrence	Average importance value	Maximum importance value
Abies balsamea	3	0.6	7.0
Acer rubrum	10	4.5	55.2
Acer saccharum	29	100.4	209.8
Acer spicatum	1	0.1	3.0
Amelanchier sp.	1	0.1	3.0
Betula lutea	16	10.9	67.1
Betula papyrifera	13	9.8	72.0
Carya cordiformis	2	0.5	8.8
Fagus grandifolia	29	96.9	244.4
Fraxinus americana	16	4.2	18.0
Fraxinus nigra	2	0.6	13.0
Ostrya virginiana	17	7.7	39.3
Picea glauca	1	0.1	3.0
Pinus strobus	9	6.6	52.0
Populus balsamifera	1	0.1	4.2
Populus grandidentata	3	1.0	18.0
Populus tremuloides	1	0.4	11.9
Prunus serotina	2	5.2	7.2
Quercus rubra	9	5.7	51.6
Thuja occidentalis	3	4.2	107.5
Tilia americana	14	5.7	25.0
Tsuga canadensis	18	33.7	198.3
Ulmus americana	6	3.6	31.8
Ulmus rubra	3	2.1	39.6

Northern Beech Stands

In the northern beech forests, sugar maple again was the only species with an importance value in all stands with beech (Table III). The next most important species, hemlock, Ostrya, yellow birch, and white ash, all were sampled in less than two-thirds of the stands, and half of the species had importance values in three or less of the 29 stands. The average importance values show sugar maple and beech to be about equal, making up approximately two-thirds of the possible value. Hemlock, although next in average importance, makes up only about one-tenth of the total value of 300, and yellow birch has a considerably lower value than hemlock. Occasionally beech occurs in stands dominated by hemlock or white cedar, but usually where beech is sufficiently abundant in a stand to be recorded at a point, it along with sugar maple dominates the tree stratum.

Sapling and seedling reproduction is usually predominantly sugar maple, with beech less abundant but much more important than other canopy species. The herb aspect pattern is similar to that of the southern beech forests. Several species literally cover the forest floor before the canopy is closed, but die back within a period of a few weeks. Important herbs sampled in spring and in summer are listed in Table IV.

For the analysis of the relationship between the beech and non-beech forests, data from the appro-

TABLE IV. Some of the most important herbs found in representative northern beech stands. The stands sampled in summer were in some cases different from those used in the spring

	SPRING		SUMMER	
	Average frequency	Maximum frequency	Average frequency	Maximum frequency
Aster macrophyllus			12.3	70.0
Claytonia virginica	17.0	60.0		
Erythronium americanum	35.5	70.0		
Hepatica acutiloba	11.0	70.0	11.9	65.0
Maianthemum canadense	24.0	70.0	20.4	85.0
Osmorhiza claytoni	14.0	65.0	15.0	95.0
Polygonatum pubescens	41.5	85.0	30.4	70.0
Smilacina racemosa			10.8	60.0
Trillium grandiflorum			14.4	50.0
Viola pubescens			13.8	70.0

priate northern or southern beech stands were combined with data taken from 40 stands used in the study of the northern conifer-hardwood forest (Brown and Curtis 1952), or with data from 43 stands used in the study of the southern hardwood forest (Curtis and McIntosh 1951). The selection of these stands was made without knowledge of location or of composition, except as a maximum range of variation in the importance value of sugar maple was sought. The reasons for the latter will be apparent in the following discussion.

In the treatment of data from several somewhat linearly related variables—in this case tree species—it is sometimes suitable to set one aside and plot the behavior of all others against changes in the one chosen. In this way the behavior of all others with respect to a single variable can be found, and the relationships of the variables to one another is indicated. In the selection of a pivotal variable—or species—it is essential that it occur in all of the samples. The species chosen can otherwise be any one of the group, but the results are most easily interpreted if the species is either at the beginning or at the terminus of the linear arrangement.

The above approach was used to analyze the data obtained in the present study. Sugar maple was thought to be the most suitable as a pivotal species because it satisfied the requirement for constancy in the samples and had the preferred characteristic of being a climax species. Within the area of beech, however, it was felt that sugar maple alone could not be used. A low importance value of sugar maple in non-beech woods of the state usually indicates an intermediate condition; in beech woods it may or may not, depending upon the importance of beech. In a particular stand sugar maple may be low in importance while beech is quite high, the result being a relatively climax woods. Obviously the behavior of most species, would be quite different in intermediate woods with little sugar maple and much oak from that in woods with a similar small amount of sugar maple but with much beech.

There is some indication in Wisconsin that beech is less climax than sugar maple (Ward 1956), but for the present purpose it may be considered close enough to sugar maple that in a general way the two species are interchangeable within the Wisconsin range of beech. The sum total of beech and sugar maple in a given woods is therefore assumed to represent a "climax unit" in which the two species may vary to produce a similar result. That is to say, the species-environment complex present in a woods composed of 60 per cent sugar maple and 30 per cent beech is reasonably similar to that in a woods of 30 per cent sugar maple and 60 per cent beech. It is not to be taken that the conditions and species are precisely the same, but rather it is intended that for purposes of comparison it is meaningful to relate other quite different species to this composite unit of relatively narrow limits. Outside of the range of beech, sugar maple alone was considered to be the climax unit against which other species could be plotted.

The data from each stand were treated in a similar manner. After subtracting the sum of the importance values for sugar maple and beech from the total stand value of 300, the individual importance values for the remaining species were taken as a percentage of the residual value. This method indicates the behavior of a species against a change in the climax unit without being mathematically dependent upon the change.

In plotting the results each species was taken separately. The ordinate value represented the per cent value the species was of the residual value, and the abscissa indicated the importance value of the climax unit. For most of the length of the abscissa the theoretical percentage value that one tree makes up of the residual value is low, but as the value of the climax unit approaches 300 the percentage rises abruptly. In view of the unwarranted weight for the chance occurrence of a single tree, only data below a value of 270 for the climax unit were considered, except where the point was based upon 5 or more trees in a total sample of 80.

That the combination of sugar maple and beech into a climax unit is a reasonable manipulation is borne out by a comparison of the behavior of a species in stands having more sugar maple than beech with the response of that species in stands in which the reverse is true. In Fig. 2, the behavior of basswood, as an example, is seen to be

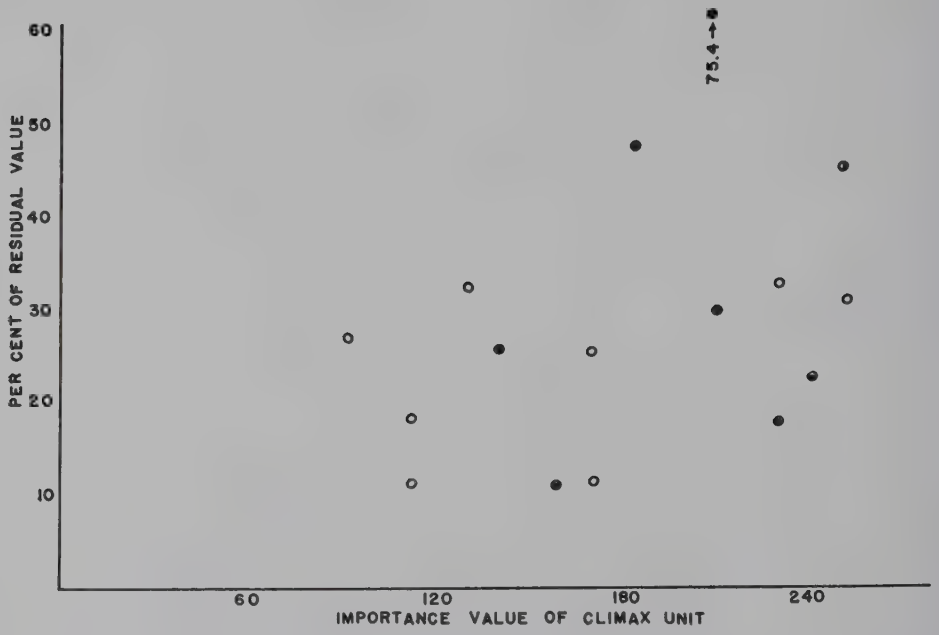

FIG. 2. The relative importance of basswood in stands having a variation in the superiority of sugar maple and beech. Circles indicate stands in which the importance value of sugar maple exceeds by at least 10 that for beech; dots indicate a similar superiority for beech. The "climax unit" is considered to be the combination of sugar maple and beech importance, and the residual value is the summation of importance values for species other than these two.

essentially independent of the varying superiority of the two dominant species.

Among the tree species that had importance values in one or more of the southern beech stands seven occurred sufficiently often to indicate a trend, while nine species were abundant enough to be used in the northern beech stands.

Importance Value Trends in Southern Beech Stands

White oak (*Quercus alba* L.) was sampled fairly often in stands in which sugar maple and beech are low in importance, but it was sampled less frequently as the climax species are more numerous. Corresponding to the drop in occurrence is a decline in importance, so that in stands with roughly 50 percent or more of the trees sugar maple and beech, white oak is of little consequence. The trend for this species indicates that the peak does not fall anywhere within the gradient of the climax unit, but occurs in more pioneer stands. There was no evidence of reproduction of this species in the beech stands.

Red oak was sampled in most of the stands that have white oak, but was also found in several stands higher up the climax unit gradient. The importance of this species is often quite high, with several values above 25 per cent of the residual value. Its occurrence in the samples dropped quite noticeably with values of the climax unit above 130. Seedlings and saplings of red oak are rare in southern beech woods.

Red elm was sampled in a majority of stands having sugar maple and beech, and seems to peak in importance where sugar maple and beech make up slightly less than half of the trees.

American elm (*Ulmus americana* L.) seldom occurs in stands that have sugar maple and beech, being sampled slightly more often in stands with sugar maple only. Elm is exceptionally low in relative importance over most of the gradient, but a few high values in the range of 150-210 result in a definite upward trend. Beyond this the behavior is uncertain because of its absence in the more climax stands. Reproduction of both species of elm is variable, but mostly unimportant in woods having beech.

White ash (Fig. 3) has a low level of importance in those stands with small values of the climax unit, but shows a rather even rise to a medium level of importance. In no stands did it constitute over 40 per cent of the residual value.

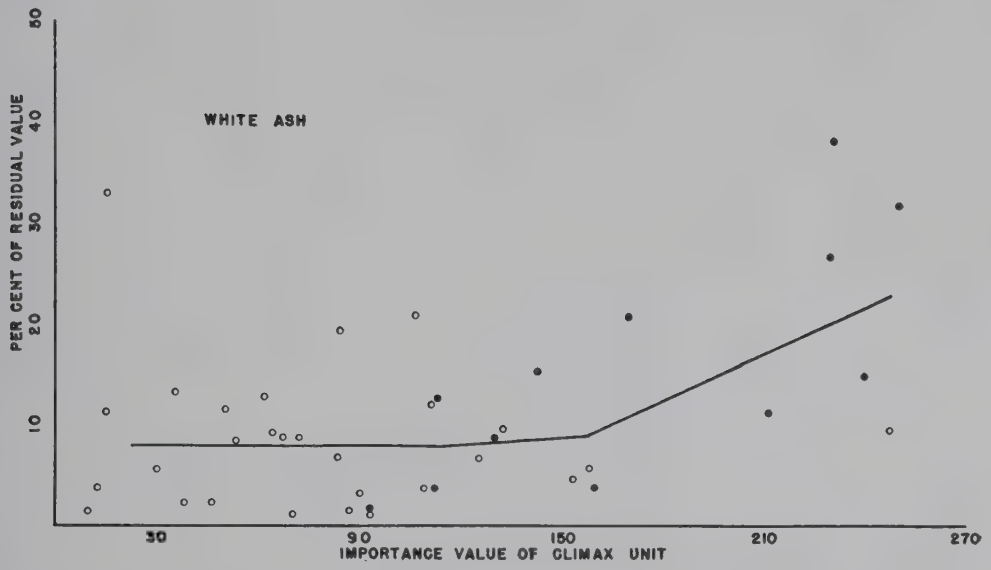

FIG. 3. The importance value trend for white ash across the non-beech—beech gradient in southern Wisconsin. Dots indicate stands that have beech; circles represent stands in which sugar maple alone constitutes the climax unit. The solid line is a running mean.

Although a fairly tolerant species, reproduction is seldom abundant in the beech woods.

Ostrya was sampled throughout the range of the climax unit, occurring in all but six of the stands, and in all but one of the stands in which the combined importance values for beech and sugar maple was greater than 150. Always below 20 per cent of the residual value in the first half of the linear increase in sugar maple and beech, several high values are found in the last half, including one stand where Ostrya was the only tree recorded at the points besides sugar maple and beech. Never a canopy species, Ostrya often makes up a large percentage of the small tree and sapling layers.

Basswood also shows high occurrence in the samples, being recorded in all but five of the stands, four of which are in the 1-30 range of the climax unit. Where sugar maple and beech occur together the chances are very great that basswood will also be found, and often in considerable amounts. The plot of the residual values indicates a gradual rise in importance as sugar maple and beech are also more important. Although found in most southern beech stands, seedlings and saplings of basswood are seldom abundant. Many of the saplings which do occur are the result of stump sprouting.

Importance Value Trends in Northern Beech Stands

In general, species other than sugar maple and beech were sampled much less frequently in the northern woods than were similar species in the southern stands, with none approaching Ostrya and basswood in the south.

White pine (*Pinus strobus* L.) seldom occurs with sugar maple and beech, but is found most often where these species are low in importance. An intolerant species, it does not reproduce except in openings of sugar maple-beech stands.

White birch (*Betula papyrifera* Marsh.), with medium sampling occurrence among the northern trees, is quite infrequent in woods with more than half of the trees beech and sugar maple. A peak in the moving average is suggested near a climax unit value of 60, with several high ordinate values in this area. From here the trend is essentially downward. White birch does not reproduce in beech stands.

Red maple (*Acer rubrum* L.) with an importance value in slightly less than half of the stands, seldom makes up more than 20 per cent of the residual value. A slight peak is suggested near the center of the gradient, beyond which this species drops both in occurrence and importance. Reproduction is occasionally quite abundant, but apparently little of it survives.

A species sampled infrequently across the entire gradient is red oak. Even so there appears to be a general rise in importance corresponding with an increase in the climax species. As in the southern beech stands, only occasional seedlings and saplings are found.

The behavior of hemock appears to be some-

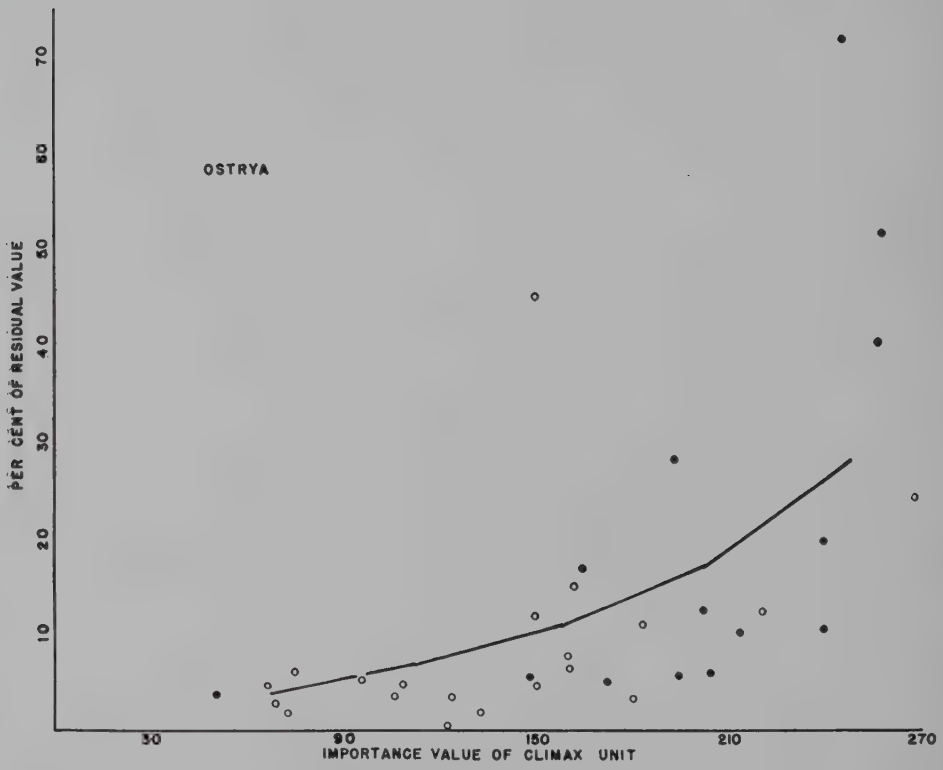

FIG. 4. The importance value trend for Ostrya across the non-beech—beech gradient in northern Wisconsin. Dots indicate stands that have beech; circles represent stands in which sugar maple alone constitutes the climax unit. The solid line is a running mean.

what irregular when compared with the presumably less tolerant species white birch, red maple, and red oak. The major peak for hemlock is at a lower value on the climax unit gradient than for any of these species. It should be emphasized that the linear treatment of data against an increase in sugar maple and beech does not necessarily indicate a linear relationship of all species plotted against this gradient. Hemlock probably enters the beech forest complex in different ways. In one case it may come in abundantly after some rather severe disturbance such as fire (Maissurow 1941) or windthrow, and attain very high importance. Beech and sugar maple gradually invade, and hemlock, while remaining higher than most other species in relative importance, shows a decided downward trend.

A second possibility is a regular successional sequence involving the replacement of less climax species. Neither mode of entry allows hemlock to maintain a high level of importance in the most climax stands. It reproduces poorly in its own shade and its saplings are heavily outnumbered by those of sugar maple and beech even where these species form but a small percentage of the tree canopy.

Yellow birch is often associated with hemlock but seldom is as important. Although reproducing poorly in stands dominated by sugar maple and beech, this species was sampled more frequently than hemlock in stands with maximum amounts of the climax species.

Below a climax unit value of 60 basswood is very rare, while above this its occurrence is quite high, and its relative importance suggests a general rise to the end of the gradient. However, basswood was again sampled rather infrequently in the stands that have maximum amounts of beech and sugar maple. It appears that basswood comes in after sugar maple is established and increases along with it, but seldom maintains itself into the most climax stands. Reproduction although usually not abundant is evidently quite successful.

White ash was rarely sampled in stands that have less than 120 as a value for the climax unit,

suggesting that it also comes in only after sugar maple and beech are well established. Above this value white ash was sampled in most of the stands, although its relative importance remains low until the last few points. Of the stands with maximum amounts of sugar maple and beech, white ash is often one of the few other trees. Reproduction of this species is nowhere abundant.

The trend for Ostrya (Fig. 4) is very similar to that of white ash except that its relative importance in the upper half of the climax unit gradient is greater. As in the southern beech stands this species is often abundant as a sapling and a small tree, but rarely grows to a diameter greater than twelve inches.

For further evidence of the relationships within the beech forests, and between the beech forests and the other upland forests of the state, data from the herbaceous layer were compared. For this purpose stands from the southern hardwood and northern conifer-hardwood forests were selected on the basis of having amounts of sugar maple comparable to the range of the climax unit in the beech forests. This seemed to be a more meaningful comparison than a random sample of all woods in these two types.

Using the same division of southern and northern for the beech forests, the frequencies for all species in all stands of a particular forest category were averaged to give a composite stand. These data were then applied in a formula presented by Motyka, Dorbrzanski and Zawadzki (1950), which allows a comparison of stands based on quantitative measures other than presence. It was employed as follows:

$$\frac{2w}{a+b}$$

with w equal to the sum of the lesser average frequencies for species in common to the two composite stands being compared, and a the sum of all average frequencies of the first stand and b the sum of all average frequencies in the second stand. Equivalent stands would give a value of 1.00.

The values obtained are most useful on a comparative basis, because depending upon the data compared the indicated degree of affinity will vary considerably; close affinity from a relative standpoint between composite stands is indicated by a smaller value than that necessary to indicate similar affinity between single stands, for instance.

The closest correlation was found between the southern hardwood and the southern beech, with a value of 0.61 indicating a considerable amount of similarity. The value of 0.51 obtained when the southern beech and the northern beech were compared was notably lower. Probably not significantly different from this is the value of 0.53 for the comparison of the northern beech and the northern conifer-hardwood forests. Decidedly lower than any of these is the calculated value of 0.37 for the association of northern conifer-hardwood and southern hardwod forests. The pattern of relationship appears to be southern hardwood—southern beech—northern beech—northern conifer-hardwood, with the herb cover rather closely related progressively, but with the first and the last quite distant. To test this order a comparison was made between the southern hardwood and the northern beech forests. If the order is correct the value obtained should be somewhat less than the value for the southern beech X northern beech (0.51), and somewhat greater than the value for southern hardwood X northern conifer-hardwood (0.37). The value obtained was 0.41 which confirms the above order.

A further comparison within the beech forests was made using early spring herb data. A value of 0.46 was obtained when the southern and northern beech forests were compared. This is somewhat less than the value obtained with summer herb data, suggesting less similarity in the early part of the growing season.

Additional evidence for the relationships between the various forest categories was found in certain soil characteristics. As with the herb data stands from the northern conifer-hardwood and southern hardwood forests were selected on the basis of having amounts of sugar maple within the range of the climax unit in beech stands. The A_1 horizon, thought to be the most indicative of vegetational influence, was used in the analysis of all factors.

The pH values of the soil samples in the various forest categories are shown in Figure 5. Although the number of stands within a category is probably not sufficient to accurately show the possible extremes, the general range of the pH for the majority of the stands is indicated. The pattern is very similar to that obtained in the herb analysis. That is, southern hardwood—southern beech—northern beech—northern conifer-hardwood, with the first two most closely related and the first and the last quite distant. The lower pH values in the north are most likely related in part to the presence of hemlock with its more acid decomposition products. Moisture holding capacity data also indicate a similar relationship of forest types, with the higher values coming in the northern forests, accountable perhaps to greater amounts of undecomposed organic matter.

A further comparison within the beech forests was made using light data; such data were not

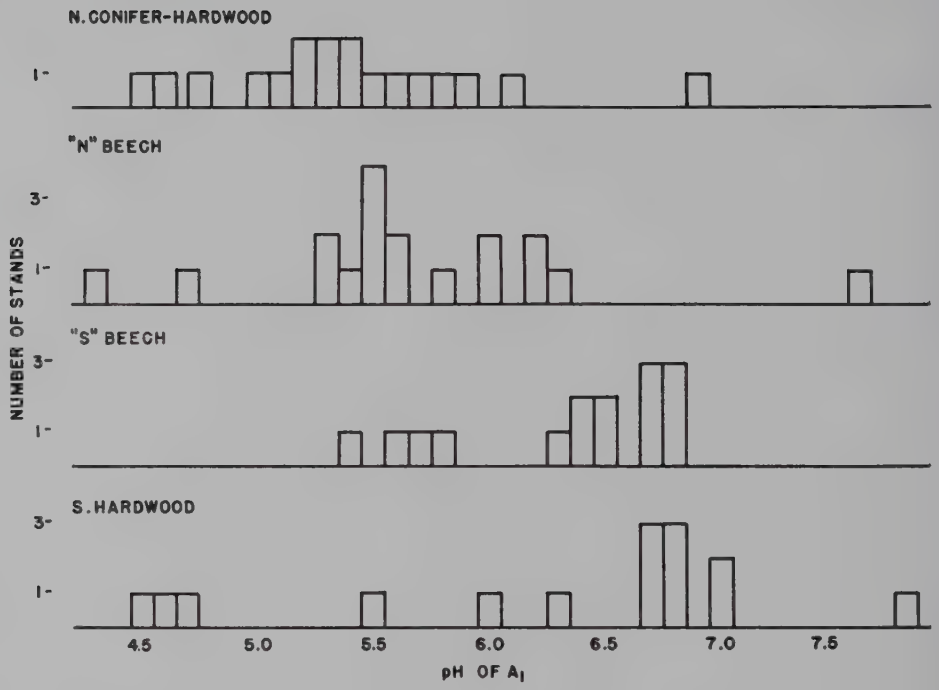

FIG. 5. pH values in the A_1 soil horizon.

available from the northern and southern upland forest studies. For this analysis it was felt that light readings in a stand could not be averaged because of the heavy influence of one or two very high readings on otherwise consistently low values. Although not widely divergent, light readings were generally lower in the northern than in the southern beech stands. The largest number of readings in the northern stands were in the intensity class of 51-100 foot candles, with over eighty per cent falling between zero and 200 foot candles. The peak in the southern stands occurred in the 101-200 intensity class, with approximately seventy per cent falling between 51 and 400 foot candles. Scattered hemlock amongst beech and sugar maple seem to result in generally low readings and this probably accounts in the main for the lower readings in the northern stands.

Discussion and Conclusions

In several recent studies in this area (Curtis and McIntosh 1951, Brown and Curtis 1952, Gilbert and Curtis 1953, Curtis 1955, Swindale and Curtis 1957) and elsewhere (Whittaker 1951, 1956) it has been found that the vegetation concerned does not segregate itself into discrete community types, but rather exists as a continuously varying gradient. The present study had as one of its primary purposes an analysis of the evidence for or against a vegetational discontinuity related to the presence or absence of beech as a member of the forest community.

Considering first the southern Wisconsin upland forests, if Sugar Maple-Basswood and Beech-Maple are distinct types, as generally regarded (Braun 1950, Oosting 1956), there should be compositional and environmental evidence to support such a division. However, when the relative importance of secondary tree species was plotted independently against the increasing gradient of terminal species importance (sugar maple or sugar maple plus beech) no discontinuity was found between the supposed forest types. The points seemed rather to indicate a continuous trend between those woods with beech and those without. The evidence from the tree stratum was therefore taken to be decidedly in favor of an interpretation of continuity.

Although herb trends along a similar gradient were not studied, the data indicate that it would be difficult to fit all herb combinations into strict Sugar Maple-Basswood and Beech-Maple categories, a gradient again being indicated. The study by Gilbert and Curtis (1953) may be cited as evidence for continuity in the herbaceous layer

in southern Wisconsin hardwood forests. The soil characteristics pH and moisture holding capacity likewise evidence a continuity between the respective forest types, suggesting that this portion of the environmental complex is very similar in climax and near climax woods whether beech is present or not.

The presence and dominance of beech, used as a basis for the separation of associations, does not bring about a significant discontinuity when the total community is viewed. On bases other than the presence or absence of this species the Sugar Maple-Basswood and Beech-Sugar Maple in Wisconsin are not readily separable types, but rather does it appear that they are part of a larger vegetational unit in which the ranges of species vary but coincident vegetational discontinuities do not necessarily result.

The contention here is not that these two types and all of the associated developmental communities cannot be separated except on this single floristic basis. At certain compositional and environmental points away from the level of intergradation the differences might well out-weigh the evidence for a gradient. The argument is rather that at the level of intergradation—the climax and near climax communities, the total evidence supports an interpretation of continuity. As designations for discrete forest associations Beech-Maple and Maple-Basswood have little validity, but the usefulness of such arbitrary designations for portions of a gradient justifies their continued usage.

With regard to the general interpretation of the beech and non-beech forested areas of the northern part of the state the problem is somewhat different. The upland forests of northern Wisconsin are generally included in a Conifer-Hardwood forest (Nichols 1935, Braun 1950, Oosting 1956) in which the absence of certain dominant species, including beech, is not used for a separation of major types, but only for the separation of sub-types or sections. The general mutuality of ranges of a basic group of hardwoods and conifers and the general similarity of climax and developmental communities within the limits of the forest area are apparently considered to overshadow any disparity in the ranges of dominant species.

Despite the absence of any claim for a major division based upon the absence of beech it is again of interest to know something of the nature of the relationship between the beech and non-beech forests in this area. Is the evidence in favor of a discontinuity or a continuity? Using, as with the southern stands the evidence of secondary species trends, herb correlations, and soil and light data it appears that in the northern forests as well as in the southern forests a vegetational continuity exists despite a floristic discontinuity involving a dominant species—beech.

A primary conclusion to be drawn at this point is that it is possible to integrate the beech forests with other upland forests of the state. In effect the continua arrangements of the southern Wisconsin hardwood forest (Curtis and McIntosh 1951) and the northern conifer-hardwood forest (Brown and Curtis 1952) may be extended to include the forests dominated by sugar maple and beech.

Of considerable interest is the possible continuity between the southern and northern beech forests of the state and a derived continuity of the southern hardwood and northern conifer-hardwood forests by way of the beech forests. Here the affinity is not so marked and the evidence is probably insufficient for any decision on continuity or discontinuity. However, it is true that the vegetational discontinuity between the northern and southern parts of the state, as brought out by Lindsey (1953), is much less obvious when the beech forest data are included in the analysis. The gap may not be bridged but the intermittent distance is greatly reduced.

Summary

The present study was a part of the intensive investigation of Wisconsin plant communities being carried out at the University of Wisconsin. The primary intent of the phase of the study reported on here was to understand the phytosociology of the beech forests of the state and the relationships of these forests to other upland forests without beech.

The beech range in the state lies entirely within the limits of Wisconsin glaciation, being confined to the eastern edge of the state. The reasons for its restriction are not completely understood, but there is some evidence that it is limited to the southwest by an unfavorable moisture regime, and to the northwest by inadequate thermal conditions. The soils of the beech forest area are mostly of the grey-brown forest type, with a tendency toward a mor humus in the northern stands and a mull humus in the southern stands.

Previous studies involving the beech forests of the state were mostly descriptive and did not consider beech throughout its Wisconsin range. According to Camp (personal communication, 1953) the Wisconsin beeches are predominantly of the red beech gene mixture, but the southern white beech and the more northern gray beech have also entered in.

The random pairs method was used to sample the tree stratum, one meter square quadrats were

used for herbs, shrubs, and seedlings, and a point count was made of saplings. Importance values were computed for trees, frequency for herbs, and relative density for saplings.

In line with previous interpretations the beech stands were divided into southern and northern categories on the basis of composition. Throughout the Wisconsin beech range the dominance of sugar maple and beech is apparent, with sugar maple tending to be more important, especially in the southern stands. In the southern stands basswood, ironwood, red oak, red elm, and white ash are of secondary importance. In the northern stands hemlock is the only secondary species of consistent importance, yellow birch, white birch, and white pine having next highest average importance values but at the same time varying a great deal in importance from one stand to another. Sugar maple saplings usually have the highest relative density in a stand, although beech predominates in some cases, particularly where root sprouting is favored.

In order to analyze the relationship of these forests to the appropriate southern and northern non-beech upland forests of the state, the behavior of secondary species was plotted independently of and against a gradient of increasing importance of a climax unit (sugar maple or a summation of sugar maple and beech). Herb correlations, and soil and light data were also used for purposes of understanding these relationships. From the various lines of evidence it is concluded that respective portions of the beech forests can be woven into the terminal ends of the southern and northern forest continua (Curtis and McIntosh 1951, and Brown and Curtis 1952), and that in southern Wisconsin the Sugar Maple-Basswood and Beech-Sugar Maple are not distinct types. The inclusion of data from the beech forests also allows a closing of the gap between the forest areas of northern and southern Wisconsin.

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WHITE CEDAR ECOTYPES IN WISCONSIN[1]

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Introduction

Within its natural range in Wisconsin, white cedar (*Thuja occidentalis* L.) displays the ability to persist in a wide range of habitats. Figure 1 indicates the range of white cedar in Wisconsin. It forms dense swamps on low, poorly drained topography and is commonly found on upland, well drained sites as well. This ability of white cedar has long been recognized and has been attributed to a wide degree of adaptability possessed by the species. Potzger (1941) has suggested that white cedar in northern Michigan possesses ecotypes because of its presence on upland and lowland sites in that area. There has not been, as yet, any critical investigation made of this phenomenon to substantiate the idea that ecotypes exist in white cedar. Taxonomically, there are no subspecies or varieties recognized in this species, there being no distinguishable morphological differences between white cedar found on any site.

This study was undertaken to determine whether ecotypic variants exist in the white cedar population in Wisconsin. In northern and eastern Wisconsin, the extremes in white cedar habitats can often be found geographically close together, sometimes within a few hundred feet. Wide geographical distances are involved in many demonstrations of ecotypes in other species. Pauley and Perry (1954) have shown that ecotypes occur in the wide ranging species of *Populus deltoides* Marsh. and *P. trichocarpa* Torr. & Gray in response to photoperiodicity. Vaartaja (1954) has determined the presence of photoperiodic ecotypes within *Pinus sylvestris* L. and *Alnus incana* (L.) Moench. as a result of studies on material collected from northern and southern latitudes in Finland. Wright (1944a, 1944b) found three ecotypes in both white ash (*Fraxinus americana* L.) and red ash (*F. pennsylvanica* Marsh.). These ash ecotypes are rather widely separated geographically and are differentiated on their ability to withstand cold.

Within a much smaller geographical area, central California, McMillan (1956) has indicated that important edaphic ecotypic variation exists in species of *Cupressus* and *Pinus* whose ranges include serpentine and nonserpentine soils. Ecotypes occurring rather close together on different soils are probably of greater ecological importance than those existing hundreds of miles apart on the same soil. The recognition of local ecotypes is of particular importance in phytosociological studies.

The procedure used in this study involved the collection, for transplantation purposes, of naturally occurring white cedar seedlings from both upland and lowland habitats throughout the white cedar range in Wisconsin, and also the collection of seed from the same sites for germination tests and growth experiments. A presentation of the methods and results will be given first for the seedling transplants, followed by a similar outline for the seed germination and growth experiments.

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White Cedar Transplantation Experiment

Comparison of Collection Sites

Figure 1 indicates the distribution of the seedling and seed collection sites. There is a total of twenty-nine sites, of which 16 are classified as typical lowland swamps consisting of nearly pure *Thuja occidentalis* with an admixture of balsam fir (*Abies balsamea*) and black ash (*Fraxinus nigra*); the remaining thirteen sites are well drained uplands, supporting in some cases pure white cedar, but often associated with hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*) and red maple (*Acer rubrum*). The lowland sites are frequently inundated during some part of the growing season, usually in spring, and tend to dry out in late summer, but still remain in a rather moist condition. The upland sites are also moist

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in the spring, but gradually become drier in summer and often are very dry in late summer and fall.

FIG. 1. Map showing the range of *Thuja occidentalis* in Wisconsin and distribution of collection sites. The range of white cedar lies north and east of the dashed line. X's are lowland sites, and O's are upland sites.

The moisture regime associated with upland and lowland white cedar habitats is the most outstanding contrasting feature. The substrate in white cedar swamps is rather uniformly composed of peat of moss and wood origin. The water retaining capacity of this peat varies from 135.1% to 513.9% (percent dry weight), with an average for all lowland collection sites of 345.5%. The soil on the upland collection sites consists of a considerably lesser amount of organic material. The upland sites are distributed on a variety of different bedrocks, but the upland soils have been derived principally from sandstones and dolomites. The water retaining capacity for the upland collection sites ranges from 33.1% to 199.1%, with an over-all average of 65.4%, less than one-fifth of the average of the lowland sites.

In regard to other soil characteristics, there is a wide variation within the lowland sites and within the upland sites. Among the lowland sites the calcium content ranges from 100 to 12,000 pounds per acre; among the upland sites the range is from 1 to 10,000 pounds of calcium per acre. The average number of pounds of calcium per acre is greater in lowland sites than in upland sites. The nutrient levels of Mg, P, K, NO_3 and NH_3 are not significantly different between upland and lowland sites. This is also true for soil acidity; the lowland sites range from pH 4.2 to pH 7.3; the upland sites range from pH 4.8 to pH 7.3.

During the early summer of 1956, a total of 360 white cedar seedlings were collected from the twenty-nine sites. Of these, 198 were collected from lowland swamps and the remaining 162 seedlings, from upland sites. The shoots of all the seedlings were between 5-10 cm in height and the root systems varied between 8-16 cm in length. It was estimated that the seedlings were in an age class of 2 to 3 years. The roots of the seedlings were wrapped in wet moss and the seedlings were placed in polyethylene bags while they were being transferred.

Within two days after collection, the seedlings were transplanted into a cold frame in the University of Wisconsin Arboretum at Madison. The seedlings were well watered immediately after being placed in the cold frame, and also periodically during the summer of 1956 in supplement to the rainfall. This additional watering was necessary to decrease the amount of seedling mortality due to the transplantation operation. The cold frame was kept free of weeds to insure the seedlings sufficient and uniform sunlight as well as to eliminate competition.

Forty-five days after being transplanted, a total of twenty-five seedlings (7.0%) had died. These seedlings were considered to have died as a result of the transplantation. This time period may seem rather long for such a determination, but very frequently a white cedar will maintain its green appearance long after it has ceased to live. Death was detectable in the seedlings when the branchlets began to curl and were easily broken off. These twenty-five seedlings were not included in the results. Survival percentages are based on a total of 335 seedlings, 188 lowland type seedlings and 147 upland type seedlings. In November, 1956, the seedlings were covered with a 15-20 cm layer of wild hay. This was done to prevent freezing and frost heaving in late winter. This protective covering was removed in April, 1957. Other than continued weed control, no other treatments were given the seedlings during the summer and fall of 1957.

Data were collected periodically beginning in August, 1956, on the survival of the white cedar seedlings. Table I summarizes the survival rates for upland and lowland white cedar seedlings. The data are given for five periods between August, 1956 and November, 1957. It can be seen from the data that the most critical period was between August and September, 1956, when the lowland seedlings suffered their greatest mortality. The difference in percentage survival between upland seedlings and lowland seedlings during that time

TABLE I. Survival of white cedar seedling transplants. Percentages are based on a total of 335 seedlings

Time Interval	PER CENT SURVIVAL		
	Upland Seedlings	Lowland Seedlings	Difference
August-Sept., 1956	89.8	76.6	13.2
Sept.-Nov., 1956	82.3	67.0	15.3
Nov., 1956-April, 1957	76.2	59.0	17.2
April-July, 1957	74.1	56.4	17.7
July-Nov., 1957	72.8	54.2	18.6

(13.2%) is statistically significant at the .01 level. During this period (August-September, 1956), the Madison area experienced a prolonged dry spell combined with high temperatures and it is thought that under these conditions the lowland seedlings succumbed, even with periodic watering. The evaporation rate at that time was probably much greater than that normally found in lowland white cedar swamps.

During the remaining periods of examination, there was a gradual increase in the mortality of the seedlings, but at a decreasing rate. In addition, the difference between the percentages of survival for upland seedlings and lowland seedlings gradually increased, with a difference of 18.6% during the July-November, 1957, period. Examination of the seedlings which had died did not disclose any definite sources of mortality. As was stated above, the immediate time of death was not readily apparent and when signs of branch curling occurred, it was probable the seedling had been dead for at least a week or more.

The results of this transplantation experiment definitely indicate that real differences exist between upland and lowland white cedar. Although it is not entirely clear from this study why the upland white cedar seedlings had a significantly higher amount of survival, it is clear that ecotypes are present and that the upland white cedar ecotype was better adapated to the conditions in the cold frame.

SEED GERMINATION EXPERIMENTS

During the second and third weeks of September, 1956, cones were collected from the same sites as were the seedlings. The cones were taken from at least five trees at each collection site to insure a representative sample. The cones were stored at room temperature (20-22°C) for a few weeks to ease the job of seed extraction; the seed was then extracted with the aid of a mechanical shaker. The seed supply for each collection site was then divided into two parts. One-half of the seed was stratified in peat which was well moistened and then placed in cold storage at 7°C. The second half was also placed in cold storage at the same temperature, but without stratification. The two groups of seed were left in cold storage for sixty days.

Petri-dish Germination Test

Germination tests were performed in the laboratory, using petri-dishes and filter paper. Two groups of fifty seeds each, for each collection site, were used. These two groups represented stratified and non-stratified seed for each site. The seeds were placed between layers of filter paper which were maintained in a moist condition during the testing period. The temperature varied between 20-22°C in the laboratory during the germination period. The petri-dishes were placed in a bright location, but never received direct sunlight. Ten days after planting, periodic checks were made to determine the amount of germination in each petri-dish. A seed was considered to have germinated when it displayed a radicle one centimeter long or longer. Data were collected for four weeks, at which time the germinations had leveled off.

The summarized results for the germination tests are given in Table II. Comparing the percentages of germination of stratified and non-stratified seeds, there is no statistical difference. Within the stratified group, the upland white cedar seed had a significantly higher percent of germination (at the .01 level) than did the lowland white cedar seed. Among the nonstratified

TABLE II. White cedar seed germination results. Part A: Total germination in Petri-dishes of cold treated seed. Part B: Germination of stratified, cold treated seed in sandy-loam soil

Part A

Seed Group	PER CENT GERMINATION	
	Upland Seed	Lowland Seed
Stratified Seed	85.3	72.8
Non-stratified Seed	77.3	76.8

Part B

Time-Days	PER CENT GERMINATION	
	Upland Seed	Lowland Seed
7	0	0
14	12.5	7.3
21	68.7	48.9
28	72.5	52.3
35	74.1	55.8
42	74.6	61.3
49	74.8	61.5

seed, there was no significant difference between upland and lowland seed germination. It seems that stratification has influenced the germination ability in a way which is not clearly understood. Under natural conditions, the seed of both upland and lowland habitats would experience a cold treatment in moist conditions, and therefore more importance should be attached to the germination results of the stratified seed. The significant difference in germination of stratified upland and lowland white cedar seed provides further evidence of the existence of ecotypes within the white cedar population in Wisconsin. There is no attempt made here to explain the cause of this difference in germination ability, but rather, to indicate the presence of the difference.

Germination Tests in Mineral Soil Plots

Germination tests were also carried out in soil plots in the Botany Department greenhouse. The germinations were made in a mixture of coarse sand and rich garden loam, which will be referred to as sandy-loam soil. Fifty stratified, cold-treated seeds from each collection site were used. The seeds for upland and lowland sites were placed in random blocks within the soil plots to lessen the effects of position on the germination results. The plots were well watered once every 48 hours and the plots were well drained. Data on germination of the seed were collected once a week for seven weeks. The results of this test are found in part B of Table II.

The difference in germination between upland and lowland seed in the soil plot is significant at the .01 level. Although the observed germination, on a whole, was not as high in the sandy-loam soil as in the petri-dishes, the same difference between upland and lowland white cedar seed is nevertheless expressed very clearly. There was no significant correlation between the germination percentages and the positions of the seed in the soil plots.

Seedling Development and Growth in Mineral Soils

In addition to germination tests in mineral soil, study was also made of the development and growth of upland and lowland white cedar seedlings in three different soil conditions. The soil in one plot was sandy-loam as described above; this plot was well drained. In the second plot, the soil consisted of pure coarse sand; this plot was also well drained. In the third plot, the soil was composed entirely of rich garden loam; this plot was poorly drained. The seedlings were derived from non-stratified, cold-treated seed, as a result of insufficient supply of stratified seed. The seed and resulting seedlings were in a random block system within the soil plots. All the plots were watered once every 48 hours during the period of this experiment. The well drained, sandy-loam soil plot remained rather moist between waterings; the well drained, sand soil plot became very dry within the 48 hour interval; the poorly drained, garden loam soil plot remained saturated at all times, frequently with standing water. The seedlings were allowed to develop under these conditions for a period of 16 to 17 weeks. At the end of this time, the seedlings were carefully removed from the plots and measurements of root and shoot development were made. The results of these measurements are summarized in Table III. Figure 2 and 3 illustrate the growth form of typical seedlings in each group. Figure 4 illustrates the relationship between the seedlings when the individual measurements for each are plotted graphically.

Table III. Seedling root and shoot development when grown under different soil and moisture conditions. Measurements were taken when the seedlings were 16 to 17 weeks old.

Soil Conditions of Plots	Average Root Length		Average Shoot Height	
	Upland	Lowland	Upland	Lowland
Pure Sand Well Drained.....	13.9 cm.	8.1 cm.	0.6 cm.	1.0 cm.
Sandy-loam Well Drained.....	19.6	7.1	1.9	1.7
Garden Loam Poorly Drained.....	4.2	7.4	1.9	2.2

Within each plot, the upland seedlings display a remarkable plasticity in their root development, producing a relatively long root system in the well drained plots and a considerably shorter one in the poorly drained plot. On the contrary, the lowland white cedar seedlings produced root systems of a rather constant size in all plots. It is evident from Figure 4 that the lowland seedlings were more influenced in their shoot development than in their root development as a result of the different plot conditions. The lowland seedlings displayed their best shoot growth in the saturated plot, under conditions very similar to those in white cedar swamps. Figure 4 also points up the difference within upland white cedar seedlings as a result of the different plot conditions. It is probably true that upland sites in nature are much more variable in their soil moisture conditions than are lowland swamps. This variability in nature could account for the plasticity demonstrated by the upland seedlings in this

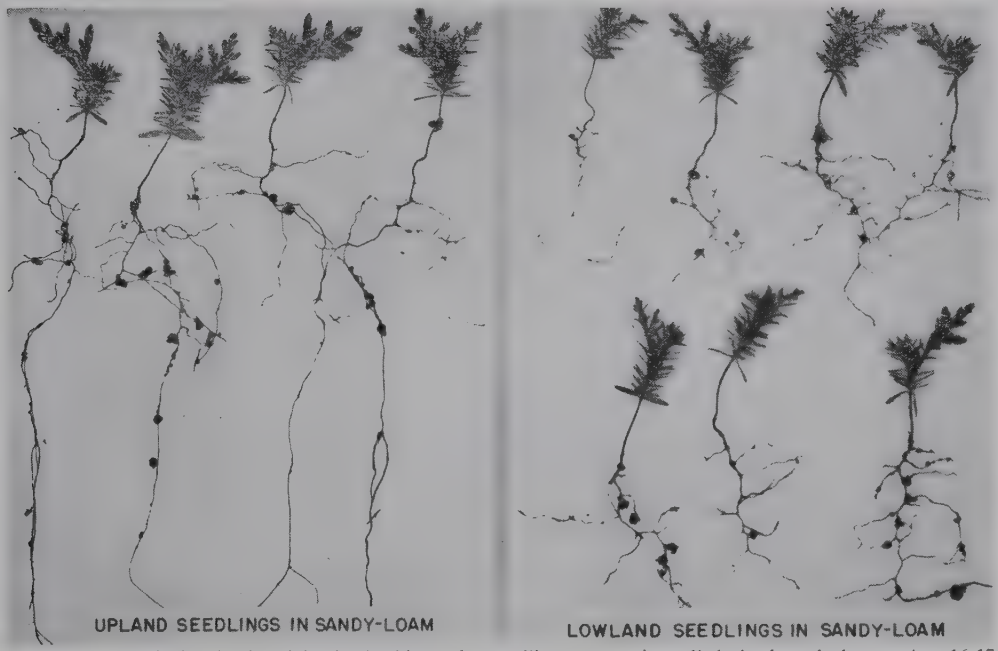

FIG. 2. Typical upland and lowland white cedar seedlings grown in well drained sandy loam. Age 16-17 weeks.

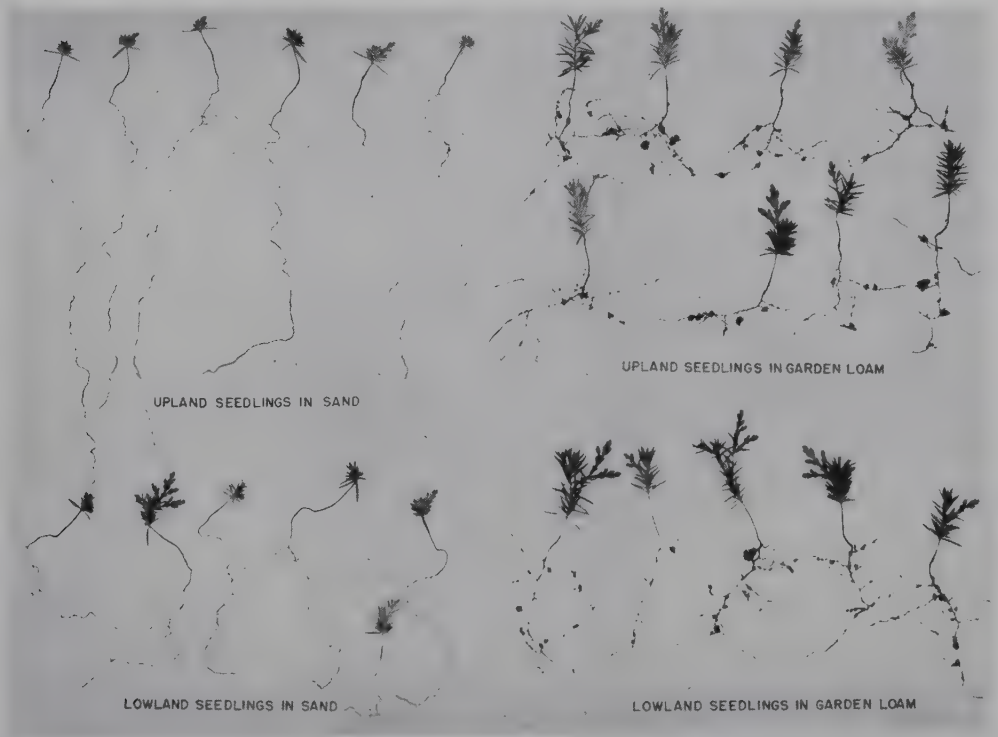

FIG. 3. Typical upland and lowland white cedar seedlings grown in well drained coarse sand and poorly drained heavy garden loam. Age 16-17 weeks.

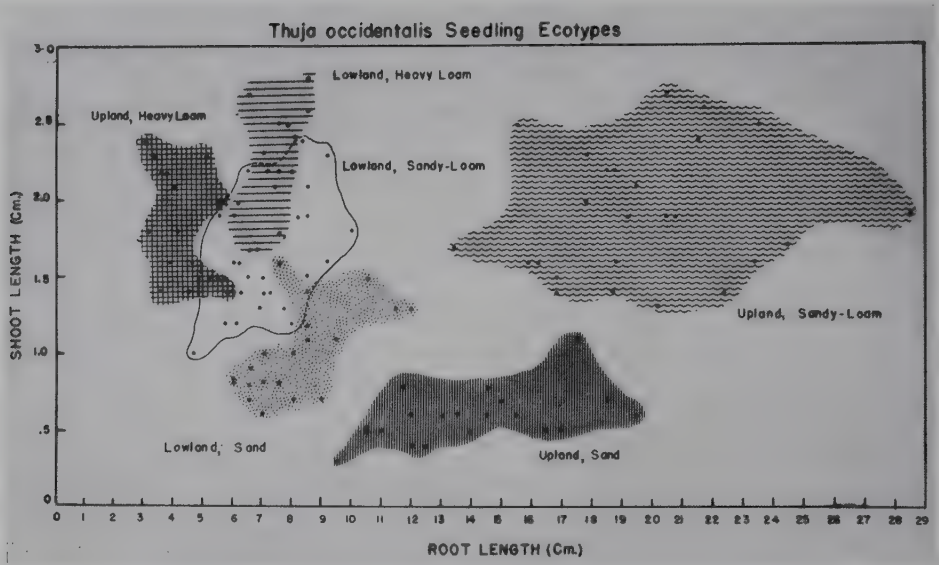

FIG. 4. Graphic illustration of white cedar ecotypes. The individual seedlings have been plotted on the basis of their root and shoot development. Each dot represents one seedling. The sand and sandy-loam soils were well drained, the heavy loam soil was poorly drained.

test. To be able to make adjustments to moisture conditions certainly is of importance in survival. In most instances, the lowland white cedar seedlings develop in rather constantly saturated or very moist conditions. It can reasonably be considered then, that the lowland white cedar seedlings are not dependent upon an excessively long or plastic root system for survival.

These results leave little doubt that genetically adapted ecotypic variants are present in the white cedar population in Wisconsin. It must be remembered that these results are from greenhouse grown seedlings and that under natural conditions other environmental factors are present which may have a modifying effect on the growth and development of the seedlings. The methods used here were of value in demonstrating the presence of white cedar ecotypes; however, these methods provide insufficient information on the exact nature of the physiological differences. The study of seedling development does suggest that moisture is a factor of great importance in the differentiation of upland and lowland white cedar.

In addition to the fact that ecotypes do occur in the white cedar population in Wisconsin, the fact that they exist within such a small geographical area is also of great significance. To the ecologist interested in phytosociological studies, the realization of local white cedar ecotypes will aid in understanding and interpreting the rather wide range of adaptation displayed by this species. The collection of white cedar seed for reforestation purposes should also be influenced by the existence of ecotypes; seed to be used for upland site re-establishment should be collected from similar upland habitats, and likewise, lowland seed sources should be used for re-establishment of white cedar on lowland sites.

SUMMARY

1. The occurrence of white cedar (*Thuja occidentalis* L.) in Wisconsin on extreme types of habitats, ranging from poorly drained swamps to well drained upland sites, suggested the possibility that ecotypic variants were present. This investigation was undertaken to determine definitely whether ecotypes exist between upland and lowland type white cedar in Wisconsin.

2. Comparison of measured habitat characteristics of upland and lowland white cedar sites indicates that the two habitat types differ most importantly in their moisture conditions.

3. Collections of naturally occurring white cedar seedlings from upland and lowland white cedar habitats were made for transplantation into a cold frame in the University of Wisconsin Arboretum, Madison. Seed was also collected from the same sites for use in germination tests and seedling growth and development studies.

4. The survival of the upland white cedar transplants was significantly higher than the lowland transplants. The germination of upland white

cedar seed in both petri-dishes and mineral soil was significantly higher than lowland white cedar seed. Growth of the white cedar seedlings in three combinations of soil and moisture gave clear indication of genetic difference between upland and lowland white cedar. The upland seedlings displayed a great plasticity in their root development, producing relatively long root systems in well drained soils and short root systems in saturated soil. The lowland white cedar seedlings displayed rather constant root development in well drained and saturated soils.

5. The results of this investigation prove conclusively that ecotypes exist in the white cedar population in Wisconsin. This situation is of additional interest in that these ecotypes occur within a relatively small geographical area. The existence of ecotypes in white cedar aids considerably in understanding the wide range of adaptation displayed by this species. In programs of white cedar re-establishment, consideration should be given to the fact that ecotypes exist and the collection of seed to be used in re-establishment should be done carefully.

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COLOR VARIATION IN THE ROUND-TAILED HORNED LIZARD, *PHRYNOSOMA MODESTUM*

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Introduction

It has become increasingly evident as a result of studies of geographic variation in organisms that the isolated or semi-isolated population is the germ from which a completely new species may often take its origin. Consideration of the various ways in which a species-population may be divided into isolated or semi-isolated parts leads to the somewhat crude division of the various isolating mechanisms into those that are succeeded by allopatric speciation, or the development of new species from populations separated by relatively impassable barriers or by great distances, and those that are succeeded by sympatric speciation, or development of new species from populations occupying the same general region, but separated by preferences for different immediate habitats within that region. The terms "geographical" and "ecological" applied either to subspecies or to isolating mechanisms have been used to imply the same difference. Although such a dichotomy is still really no more than hypothetical, it has a certain usefulness in emphasizing that the scale of geographic isolation may vary enormously, and that isolation may sometimes result from strictly non-geographic determinants, such as seasonal or diurnal variations in breeding activity (Mayr 1942, p. 189 *et seq.*).

The search for examples of ecological subspecies is complicated by the fact that the conditions found in different habitats occupied by members of a given species may have direct effects upon individuals and succeed in producing distinct "ecophenotypes" from a single genotype. Although such variants are interesting from the standpoint of environmental physiology, they have no immediate significance to the student of evolutionary processes. The same search is simplified if the "subranges" or special habitats occupied by ecological subspecies are capable of being objectively described and distinguished from one another. If the structure of the variation among the subspecies can be related to the structure of variation among the subspecific habitats some insight may be gained into the relative effects of selection and drift in producing the variations.

The desert is a favorable locale in which to study the formation of ecological subspecies and has in fact already received attention in this regard. Often the immediate habitat of a desert animal consists of little else that a bare soil or rock surface with relevant attributes such as color, temperature, and texture which are relatively easy to describe exactly. The complications often offered

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by vegetation are minimized. Animals living in such an exposed habitat frequently show striking adaptations to precisely the describable attributes enumerated above, of which concealing coloration, particularly among small or slow-moving forms, is an example. For this reason, the study of variation in color among smaller desert animals has yielded some of the most interesting information on the possible steps preliminary to the formation of ecological subspecies. Dice and Blossom (1937), studying color-variation in *Peromyscus* and certain other mice in southwestern United States, have shown that there is a strong correlation between the pelage-color in local races and the color of the soil or rock on which they are found, an observation similar to that of Benson (1933), who used a less precise means for comparison of colors. That such variation in color has a genetic basis was quite clearly shown by Sumner (1930), who worked with *Peromyscus* under roughly analogous circumstances in southeastern United States (see also Sumner 1926). The latter work also demonstrated that the differences in color that characterize subspecific populations, and which generally appear to be adaptive, may be accompanied by heritable and seemingly nonadaptive differences in numerous morphometric characters.

It would be valuable to extend such investigations to other vertebrate species, among which the relatively rich and varied reptile fauna of the American desert offers many suitable possibilities. We have selected from among these *Phrynosoma modestum* Girard, the round-tailed horned lizard, a small slow-moving species found on open sandy or gravelly alluvium at low altitudes through the region shown in Figure 1. It is apparently a species that depends primarily upon concealment for protection; approached or alarmed, it flattens and crouches in place, not running away or showing aggressive responses. Excepting a few darker crossbars on the tail it is uniformly colored dorsally, but varies noticeably in hue from place to place (Lowe 1947). Its range is transected by the Rio Grande and Rio Pecos, by numerous smaller streams and stream-valleys and by the Rocky Mountains. Within it are several distinct soil or rock types. In New Mexico east of the Pecos and west of the edge of the *Llano Estacado* these are generally red (Mescalero alluvium); between the valley of the Pecos and the Rocky Mountains they are generally gray. In the Tularosa Basin west of the mountains they may be black (*Malpais*), white (gypsum) or variously gray or brown; similar variation is to be found in the *bolsons* inhabited by the species south of the Rio Grande. Such latitude in color might be expected to invite the tendency for a sedentary species to become divided into local races, colored like the local soils and perhaps showing other differences unrelated to particular environmental attributes.

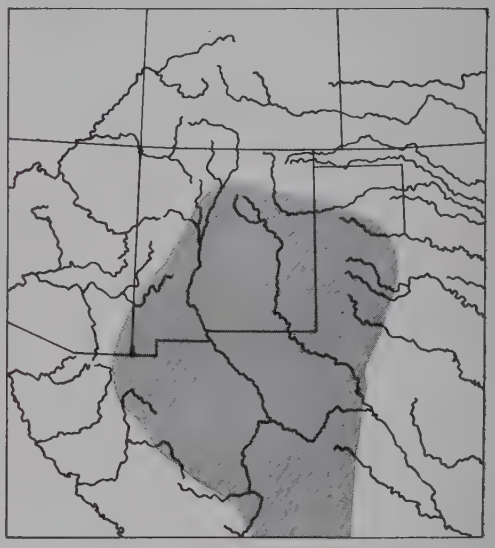

FIG. 1. Map of New Mexico and portions of adjacent states, showing the range of *Phrynosoma modestum* (after Smith, 1946). The Rio Grande divides the range completely, the Rio Pecos almost completely.

The problem of color-adaptation in reptiles is somewhat confused by the fact that they, unlike birds and mammals, are supplied with pigmentary effector systems that enable individuals to change color, sometimes very rapidly. Such color-change may be invoked as a means of concealment for an individual moving from one background to another, although this has not been decisively demonstrated for any species of lizard (see, however, Sumner 1934 and 1935). The evolution of such a mechanism (denied to birds and mammals) would seem to take precedence over the genetic fixation of one particular color, however well matched to the background, under any environmental conditions whatever, or at least in any environment in which the background color is not absolutely uniform from place to place within the area ordinarily covered in the excursions of a single individual throughout its life. Extreme caution is therefore necessary to distinguish between the development of a more efficient pigmentary effector system and the development of more precise but inflexible duplication of background color.

Further confusion appears when the thermoregulatory function of the pigmentary effectors is

taken into consideration. Depending upon the relative stresses applied to a species by temperature and predation, one might sometimes expect to find selection carrying a local population away from direct adaptation to background color. However, because the thermal conditions experienced by an animal living at the surface of the ground are also a function of soil color, one might still find local background color exerting a powerful effect upon color-differentiation of local races, though not necessarily acting to produce color-resemblance. The possibility that thermoregulation and color-adaptation are thus connected means also that it is important to use some care in making observations in the field, where apparent adaptedness or correlation with background color may be quite different at different points in the daily temperature cycle. The same possibility must be considered when observations are made in the laboratory, where results may be affected by internally-controlled rhythms in color-change originally corresponding to rhythms in environmental temperature-change.

This paper describes a study in the field of the colors of local populations of *Phrynosoma modestum* in relation to the colors of local soil, along with some laboratory observations made in an effort to identify some of the nongenetic determinants of skin-color in this lizard. It is based upon a portion of a dissertation (by R.E.B.) submitted to the University of Wisconsin in partial fulfilment of the requirements for the degree of Doctor of Philosophy. We are grateful to Delbert E. Meyer for valued assistance in the field, to the Research Committee of the University of Wisconsin and the Wisconsin Alumni Research Foundation for generous and continuous financial support, and to the New Mexico Military Institute for allowing us to use some of their facilities.

Methods

Description of Colors of Lizards and Soils

It has been the common practice in biological literature to describe the color of a surface by matching it to one of the samples in a standard color-chart (such as Ridgeway 1912). This method is unsatisfactory for numerous reasons that need not be discussed in detail here, save to mention that it provides no quantitative or numerical means for comparison of two colors, suffers from the abundant defects in human color-vision and does not provide a stable reference, inasmuch as standard color-charts are difficult to reproduce in the first place and tend to show changes with use or aging. The chief requirements of an improved method would be that it provide descriptions of color in numerical form,

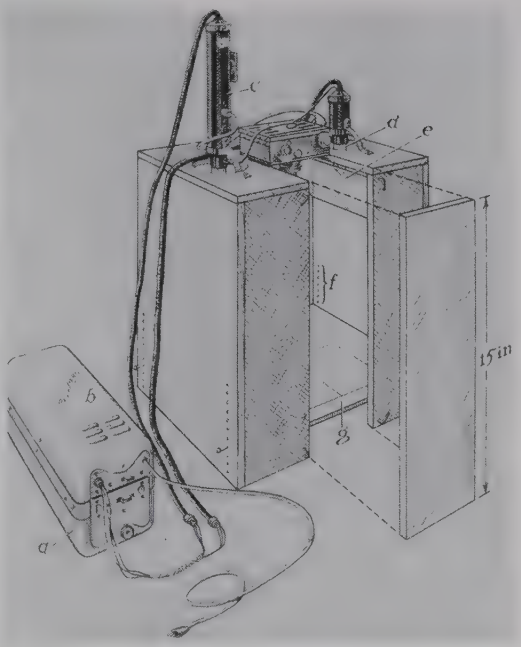

Fig. 2. Drawing of apparatus in which photographs of specimens were made. Details are explained in the text.

that it function independently of the physical condition of the observer and that it refer to an unchanging standard.

The "color" of a surface is completely and uniquely specified if the relative intensity of reflection from it at each wave-length of the incident light can be stated under any particular set of conditions. The necessary determinations could be made with a spectrophotometer, and would be referred to collectively as a complete reflection spectrum. Such a c.r.s. could be approximated by measuring the relative intensity of reflection from the surface of light passed through the members of a series of filters with monochromatic or near-monochromatic transmission bands (such as interference filters). The construction of a complete or approximate reflection spectrum generally requires apparatus that cannot be taken into the field.

A second method, quite different from the first in principle, is to match the unknown color with one produced by mixing light from three differently-colored sources (i.e. by mixing the correct proportions three "primary" colors). The colored sources in this instance need not be monochromatic. The set of three numbers corresponding to the relative intensities of the three sources required for duplication of the unknown color constitute a description of the color. Such a method may be applied in a slightly different way by

measuring the relative intensities reflected by the uniformly illuminated surface through three filters of known but not necessarily monochromatic transmission characteristics. The eye may be looked upon as though it used such a "method" for color discrimination. It is important to notice that this method does not distinguish the same "colors" that are distinguished by different reflection spectra. It can be shown quite easily that any one of an infinite set of different reflection spectra will give the same set of three numbers representing relative intensities of the members of any particular group of three primaries, whether these are filters or light sources. The eye suffers from the same deficiency, failing to distinguish individually all c.r.s.

Assuming a simple trichromatic mechanism of color-vision in man or in any other organism, it would be possible, by properly choosing the primaries, to obtain a color measurement corresponding in every case to that obtained in the eye of the organism in question, i.e. to obtain sets of index numbers that would successfully distinguish among all colors distinguishable by the eye, and confuse only those not visibly different. Finding such primaries for the human eye would be the central problem of finding an additive method of photographic color-reproduction. An arbitrarily chosen set of primaries will not in general give the same results as a particular eye, i.e. it will detect differences between colors not visibly distinguishable and will confuse others that appear distinct. It is worth noting that any two surfaces having the same c.r.s will appear to be of the same color to any eye, regardless of the colors of its primaries.

The second method has been used in this investigation, largely because of the relative ease with which requisite determinations could be made in the field. The set of primaries used here has been chosen so as to approximate roughly the apparent primaries of the human eye, but the choice was made without the object in view of achieving an exact correspondence. In a study of predation and protective coloration it would ordinarily be of considerable advantage to use a method of color-discrimination exactly the same as that used by the predators themselves. In theory this could be arranged, provided certain relevant data were available; lacking the data, we have had to proceed without such a refinement.

The general method we have used is to take four photographs under reproducible conditions of each specimen whose color was to be described, one through each of a set of three colored filters and one without a filter. The photographs were taken in the apparatus shown in Figure 2. Specimens were placed on the stage (g) which could be raised or lowered for adjustment of focus by changing the positions of its supporting pins (f). An Argus C-3 35-mm camera was used as filmholder, lens system and shutter. Illumination was provided by two krypton-xenon Geissler tubes energized by the discharge of a condenser (b) which was charged either with 115-V line current or with 1.5-V dry cells. Provided the condenser charge is always the same, such a source is very constant with regard both to the quantity of light energy and the quality of the illumination furnished. If dry cells are used as a source of energy, the whole apparatus may be taken anywhere and used easily in the field without sacrifice of efficiency. The Geissler tubes themselves were covered with screens of frosted glass (e) to diffuse the light and reduce its intensity; further diffusion was achieved by painting all internal surfaces of the box white. Exposures were made at f:16 with the shutter open for 0.02 sec., the discharge flash (approximately 0.001 sec.) actually timing the exposure. The filters used were Wratten No. 15 (yellow), No. 47 (blue) and No. 25 (red); their transmission characteristics are given in Table I. In addition to the filters, a +3 portrait lens was placed in the system to reduce the focal distance of the camera lens.

TABLE I. Properties of filters, emulsion and light-source used for making colorimetric measurements

Wavelength (mμ)	Fraction of incident light transmitted by filters			Emulsion sensitivity × emission intensity (units arbitrary)
	Red	Yellow	Blue	
440	0.000	0.000	0.503	1.099
450	0.000	0.000	0.483	1.071
460	0.000	0.000	0.434	1.058
470	0.000	0.000	0.362	0.957
480	0.000	0.000	0.285	0.762
490	0.000	0.000	0.196	0.657
500	0.000	0.000	0.113	0.559
510	0.000	0.010	0.056	0.598
520	0.000	0.160	0.019	0.682
530	0.000	0.521	0.004	0.790
540	0.000	0.707	0.000	0.706
550	0.000	0.843	0.000	0.783
560	0.000	0.875	0.000	0.781
570	0.000	0.887	0.000	0.773
580	0.000	0.893	0.000	0.735
590	0.126	0.897	0.000	0.666
600	0.500	0.900	0.000	0.569
610	0.750	0.901	0.000	0.550
620	0.826	0.902	0.000	0.581
630	0.855	0.903	0.000	0.510
640	0.867	0.904	0.000	0.366
650	0.876	0.905	0.000	0.331
660	0.882	0.906	0.000	0.250
670	0.885	0.906	0.000	0.200
680	0.890	0.907	0.000	0.150

Film used for all determinations was Dupont Type 904 B "Superior" 1, 35 mm. This is a slow (ASA exposure index 20-25) fine-grained pan-

chromatic film with a relatively heavy fog. Because of the high light intensity produced by the two tubes, it has been necessary to use a slow film, but in future work it would be better to use a film with lighter fog, perhaps one of the types used for spectrographic analysis. Estimates of the chromatic sensitivity of the film and the spectral distribution of the light from the tubes were obtained by exposing samples of the film to light from the tubes in a grating spectrograph. Densities in the developed image of the spectra obtained were determined with a standard spectrographic densitometer; these are recorded in Table I as the product (in arbitrary units) of emulsion sensitivity and emission intensity. Film was usually purchased in 100-ft lengths and cut and wound on smaller spools as needed; when not in the camera, film was stored in a refrigerator in airtight containers provided with desiccant.

Exposed films were developed in large batches (160 to 480 frames at a time) in Microdol at 68°F, with the time of development adjusted to the age of the developer so as to maintain an approximately constant value of γ. Following development, densities of the specimen images were determined in a Beckman DU spectrophotometer. Sections containing areas of interest were clipped from the developed films and these placed in the holder shown in Figure 3, which in turn fitted into the standard cuvette carrier of the spectrophotometer. A densitometer for spectograph plates or films might have been used as well.

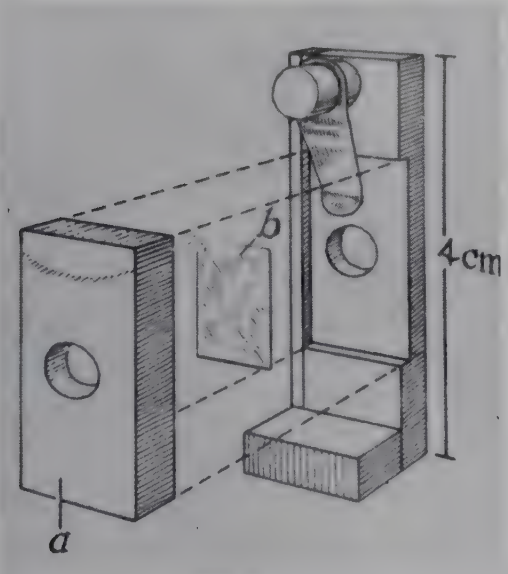

FIG. 3. Holder for small sections clipped from photographs of specimens during spectrophotometric determination of density.

Transmission readings of the specimen films were compared with transmissions obtained through negatives made by photographing a standard white cardboard surface through the same set of filters. All "standard reflectances" given below are ratios of the intensity of the light reflected from the specimen to the intensity of light reflected from such a standard surface under the same conditions. Such values were obtained by noting that density of the developed image (where density is the negative logarithm of the fraction of incident light transmitted by the silver deposit in the film) is approximately proportional to the logarithm of the intensity of the illumination incident on the emulsion at exposure. If these relations hold, then the ratio of the intensity of reflected light from the surface of the specimen to the intensity of reflected light from the standard white surface will be given simply by the ratio of the percentage transmission through the developed image of the white surface to the percentage transmission through the image of the specimen. The standard white cardboard has been compared with a freshly-smoked MgO surface, with the following results:

	No Filter	Red	Yellow	Blue
Reflection from White Cardboard Relative to MgO.....	0.94	1.07	0.82	0.77

It is unimportant, except for purposes of expressing the reflectances from the specimens in units that are the same in all parts of the spectrum, that the standard surface be precisely "white" or even as "white" as a MgO surface. The slight excess of reflection toward the red end of the spectrum from the cardboard surface may be the result of the incorporation of a fluorescent optical bleach in the surfacing of the paper, although in this instance, 1.07 does not represent a significant departure from 1.00.

Photographs of the working standard were made frequently, such that at least one set of photographs of the standard occurred in each small roll of film used (about 20 frames). In all instances, every set of specimen photographs was accompanied by a set of photographs of the standard that had been stored and developed under identical conditions, and that had originally come from the same batch of emulsion.

A method very similar to this one has been used by Crane (1954) for describing the colors of butterfly wings. Instead of computing the reflectances of her specimens from the density of the image of a single standard, she obtained them directly by comparison of the density of the specimen image with the densities of the images of the steps of a

gray-scale always photographed on the same frame as the specimen. Her technique is likely to yield somewhat more precise results than ours, but is considerably more laborious. Neither method is completely satisfactory for very critical work unless certain special precautions are taken. In prinicple, this is also the method used by Sumner (1927).

There are two kinds of error inherent in a method of this kind; one of them has to do with the validity of application of the theory outlined above, the other with the reproducibility in behavior of the materials used.

For most photographic materials, the relation between the logarithm of incident intensity and image density is not ordinarily a perfectly straight line, but is rather an S-shaped curve, such that at extremely low incident intensities the image density is actually somewhat greater than would be expected from a linear relationship, and at extremely high intensities it is less than would be expected. The range of intensities over which the relation is linear or very close to linear varies considerably from one emulsion to another. In using a simplified method of computing from emulsion densities, we have thus tended to bias *upward* the low intensities and *downward* the high ones. Since the reflectances of our specimens are all expressed relative to the reflectances of a standard white surface with reflectivity high across the entire spectrum, our relative reflectances are commonly too high. For the time being we have not attempted to correct for these difficulties, although this would be possible following a careful study of the behavior of the particular photographic materials used. Our interest lies primarily in comparing reflectances from lizards and soils, both of which would be affected by the same errors; the effect of the bias would be to conceal small correlations, but not to exaggerate any. Finding a correlation, then, we may be relatively certain that there is one; failing to find one, we cannot be sure that one does not in fact exist.

It should be noted also that the simplified computation we have used is valid only for the situation in which the slope of the straight part of the incident-intensity: density-of-image curve (γ) is equal to 1.00. The value of γ is controlled by varying the time during which the developing reagents are in contact with the emulsion, and can be determined from the densities of the images of the steps of a calibrated gray-scale. Corrections for variable γ may be introduced into our computations by noticing that the computed ratio of specimen reflectance to standard reflectance is the true ratio raise to the power γ. The computed ration is corrected to the true ratio by raising the former to the power $1/\gamma$.

The sources of error arising from failure of the photographic materials to behave reproducibly may be classified as follows:

1. Variations in quality of different batches of emulsion, which may affect the transparency of the emulsion vehicle, the degree of fogging, the characteristics of the intensity: density curve or the response of the emulsion to particular conditions during development.
2. Local irregularities in emulsion behavior, producing difficulties of the kinds listed above and resulting in variation in behavior from one section of a single piece of film to another. Such irregularities may be in the form of gradients along considerable lengths of film, or may occur simply as irregularities over short distances.
3. Irregularities in lighting within the photographic apparatus, tending to produce spurious differences between similar objects not placed in exactly the same position under the lights and lens.
4. Failure of conditions during development to be precisely duplicated from one batch to another, or even everywhere within a single batch. Here such variables as temperature, age of developing reagents and thoroughness of mixing in the development tank are of importance.
5. Failure of the spectrophotometer to provide the same value for the density of a given specimen measured more than once.

Some of these sources of error have been compared by analyzing the variance of a set of readings taken from a large number of photographs of the same white cardboard surface. The readings were distributed over samples of film associated with two emulsion batches and several development batches, and could be classified so as to make it possible to compare variances between and within forty-frame strips of film (a standard "roll" as we have used the term), between and within single frames and among individual readings made on the same sample clipped from a single frame. The result of the analysis is given in Table II. Additional variance components are apparently not introduced from one development batch to another; there are, however, differences from one batch of emulsion to another, and within the single emulsion batches such as to affect both roll and frame means. Within a single frame, variation is entirely explained by errors in the spectrophotometric determination of density. Reduction of the significant errors would demand that critical comparisons be made from material preferably taken within a single frame. In this

TABLE II. Analysis of variance of absolute reflectances from standard white cardboard surface

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F
Part I. Test of differences among emulsion batches				
Total	251	1,813.227		
Filters†	3	1,719.810		
Emulsions within filters	4	16.542	4.135	13.13*
Error	244	76.875	0.315	
Part II. Tests of other factors (all data from a single emulsion)				
Total	203	1,528.546		
Filters†	3	1,467.293		
Within filters	200	61.253		
Among development batches within filters	8	2.582	0.323	1.06
Within development batches	192	58.671	0.306	
Among 40-frame rolls within development batches	40	29.084	0.727	3.73*
Within rolls	152	29.587	0.195	
Among single frames within rolls	28	24.630	0.880	22.00*
Within frames	124	4.957	0.040	
Among clippings on a single frame	40	0.927	0.023	0.50
Among duplicate spectrophotometer readings on same clipping	84	4.030	0.048	

†Including readings taken without filter.
*Significant at the one-percent level.

regard, it would be well to have had a sample of the standard white surface in each frame for comparison with the specimens within that frame. Our comparisons were always made with white standards included in the same roll with the specimens.

Collection and Treatment of the Animals

Lizards were collected during the summers of 1953, 1954 and 1955 over as much as possible of the range of the species. A very large number of specimens came from Lincoln and Chaves Counties, New Mexico, an area in which they appear to be particularly abundant.

The animals were located from a moving automobile and run down and captured by hand. At the place were each specimen was taken, a sample of surface soil was collected. Upon capture, the lizards were placed in numbered cloth bags and kept in the car out of the sun. They were not found to be active before about 8:00 A.M.; collecting usually began at about that time and ended at about 11:00 A.M., when they retired. All lizards captured during such a three-hour period were photographed at the end of the period; their toes were then clipped to identify them as individuals and they were placed in holding cages for transport back to the laboratory in Madison, Wisconsin. Because the lizards became active again later in the day, a short collecting run was often made between 4:00 and 6:00 P.M. during which the same procedure was followed. Localities for lizards and soil samples were recorded to township and section or nearest minute of latitude and longitude. Soil samples were photographed later in air-dry condition in the same apparatus used for photographing the lizards. The soil was simply poured out of its container into a shallow tray and photographed without additional treatment. For each lizard or soil sample a set of four relative reflectances was assembled according to procedures outlined above.

RESULTS OF THE FIELD INVESTIGATIONS

For comparison of the reflectance values obtained for the lizards and corresponding soil samples we have used linear correlation coefficients. The results for all specimens collected in the three years are given in Table III. They indicate moderately strong correlations in total albedo (no filter; results here are, of course, relative to the spectral distribution of emulsion sensitivity × emission intensity given in Table I, and do not refer to albedo in sunlight) and in reflected light passing through the yellow filter. There are weaker but still significant correlations for reflected light passing through the red and blue filters.

TABLE III. Coefficients of correlation between relative reflectances of dorsal side of *Phrynosoma modestum* and soil at locality of capture

Filter	r	Number of specimens
Total collection, 1953-1955:		
None	0.566†	85
Red	0.273*	82
Yellow	0.360†	85
Blue	0.235*	82
Newly-hatched animals, collection of 1955:		
None	0.099	21
Red	0.101	20
Yellow	−0.182	21
Blue	0.399	21
Half-grown animals, collection of 1955:		
None	0.502	12
Red	0.346	10
Yellow	0.117	12
Blue	0.544	11
Adult animals, collection of 1955:		
None	0.894†	8
Red	0.289	9
Yellow	0.825†	9
Blue	0.575	9

*Significant at 5-percent level. †Significant at one-percent level.

It should be recalled that, had the relative reflectances for lizard and soil been exactly the same for all filters, an exact match in color would nevertheless not have been indicated, but simply indistinguishability to a simple trichromatic eye operat-

ing with primaries of characteristic spectra the same as those of the filters used in the apparatus, and thus something close to indistiguishability to the human eye. Had all the correlation coefficients been exactly 1, a precise colormatch would for this reason not necessarily have been implied.

The exact significance of the correlations may best be seen from a further amplification of this point. Suppose we take a surface with a given c.r.s. and generate the c.r.s. for another surface by multiplying every intensity in the reflection spectrum of the original surface by a constant, k. If we now observe each of these two surfaces with a theoretical trichromatic eye in which effect is proportional to luminous flux or with an apparatus like the one we have used, the two will appear to have the same "color" (chromaticity and saturation) but, depending upon the value of k, one of them may appear brighter than the other, i.e. the ratios of the intensities reflected from the two surfaces will be the same for all three filters. If we now construct several such pairs, beginning with a different c.r.s. each time, but always using the same value of k, and then compute a correlation coefficient as we have done for the soil-lizard pairs above, we will obtain a value of exactly 1 no matter what value of k has been used. If $k = 1$, then the corresponding reflectances for the two surfaces will be numerically equal; if $k \neq 1$, corresponding reflectances will not be numerically equal, but the correlation will be perfect for any value of k. Here "similarity" of the colors (chromaticity and saturation) of the two members of each pair would be independent of the choice of primaries for the eye or apparatus. An animal that adjusted its skin color according to such a scheme would be protectively colored (again, in the sense of chromaticity and saturation but not brightness) in the sight of any predator, regardless of the characteristics of its visual apparatus.

Perfect correlations may also be obtained through another kind of transformation. If we begin again with a surface having a given c.r.s. we can generate c.r.s. for another surface also by multiplying every intensity in the reflection spectrum of the original surface by a coefficient that is not a constant but rather a function of wavelength. Two such surfaces will not generally appear to have the same color when observed by an eye with an arbitrary set of primaries. However, there is at least one set of primaries for which the colors will appear to be the same; the characteristic spectra of these primaries can be found if the value of k is known for each wavelength. Thus, if a set of primaries be chosen in advance, it would be possible to construct a set of paired surfaces as above, by choosing the values of k appropriately in each instance, such that the correlation coefficient computed in the same sense as above would be equal exactly to 1. Here, however, the apparrent similarity in color between the members of the pairs depends entirely upon the characteristics of the primaries; if a different set of primaries were substituted, the correlation would be altered. An animal that adjusted its skin color according to such a scheme would be protectively colored only to one particular kind of eye.

Our data are insufficient to distinguish between these two cases. A closer study of the relationships using several sets of primaries may be expected to clarify the situation. On the other hand, we can note that the latter case is *a priori* a rather improbable one and, rejecting it for the moment, look upon the significant correlations as suggesting a similarity in the form of the c.r.s of the lizards and soils. For reasons that are obvious by this time, it is not possible to describe the similarity in terms of the direct visual experience of a predator unless something is known of the mechanics of its visual apparatus or until enough information is available to choose the first case unambiguously.

Two general conclusions seem justified at this stage: (1) that as soils become generally darker or lighter without regard to color, the lizards tend to do the same, and (2) as the soils change color from place to place, there is a tendency for the lizards to show similar changes. This does not imply that the lizards are equally distinguishable or indistinguishable from the soils at any particular level of color in the latter. Total albedo is matched with greater precision than albedo within any of the selected fractions of the spectrum.

Some mean intensities of reflection for lizards and soils are shown in Table IV. They show a tendency for lizards to be paler than their substrata, in contrast to the mammals studied by Dice and Blossom (*op. cit.*), all of which were found to be darker than the soils on which they occurred. It is probably significant in this connection that the mammals were primarily nocturnal or at best crepuscular species, whereas the lizards are strictly diurnal, not becoming active until the sun has been above the horizon for several hours. In the latter one would expect to find a diel cycle in albedo characterized by a minimum at the end of the morning period of activity and at the beginning of the afternon one, times when temperatures at the surface of the ground are maximum and the lizards are active, with perhaps a maximum during the cooler parts of the active period. Because our collecting depended upon visibility, thus movement, of the animals we have probably biased our results somewhat in favor of high albedo.

TABLE IV. Mean standard reflectances of the dorsal side of *Phrynosoma modestum* and soil in various localities

Locality	No filter	Red	Yellow	Blue
	Soils			
New Mexico				
Chaves County				
T11S, R22E (West of R. Pecos)	0.268 ± 0.020	0.321 ± 0.022	0.323 ± 0.018	0.306 ± 0.011
T11S, R23E (West of R. Pecos)	0.248 ± 0.006	0.298 ± 0.009	0.295 ± 0.003	0.293 ± 0.004
T10S, R26E (East of R. Pecos)	0.255 ± 0.009	0.302 ± 0.024	0.270 ± 0.020	0.260 ± 0.018
T10S, R27E (East of R. Pecos)	0.265 ± 0.017	0.296 ± 0.018	0.302 ± 0.019	0.290 ± 0.012
Lincoln County	0.227 ± 0.012	0.339 ± 0.047	0.290 ± 0.026	0.303 ± 0.023
Guadalupe County	0.204 ± 0.007	0.266 ± 0.004	0.232 ± 0.014	0.256 ± 0.010
De Baca County	0.260 ± 0.030	0.270 ± 0.010	0.280 ± 0.024	0.284 ± 0.001
Texas				
Hudspeth County	0.345 ± 0.071	0.448 ± 0.036	0.421 ± 0.041	0.340 ± 0.018
Mexico				
Ciudad Chihuahua	0.162 —	0.209 —	0.219 —	0.197 —
	Lizards			
New Mexico				
Chaves County				
T11S, R22E (West of R. Pecos)	0.468 ± 0.037	0.529 ± 0.018	0.532 ± 0.056	0.471 ± 0.030
T11S, R23E (West of R. Pecos)	0.433 ± 0.034	0.504 ± 0.034	0.522 ± 0.095	0.506 ± 0.009
T10S, R26E (East of R. Pecos)	0.433 ± 0.060	0.472 ± 0.010	0.458 ± 0.034	0.400 ± 0.002
T10S, R27E (East of R. Pecos)	0.511 ± 0.018	0.553 ± 0.039	0.550 ± 0.026	0.471 ± 0.034
Lincoln County	0.310 ± 0.023	0.414 ± 0.047	0.396 ± 0.075	0.372 ± 0.060
Guadalupe County	0.424 ± 0.068	0.724 ± 0.076	0.666 ± 0.098	0.532 ± 0.026
De Baca County	0.556 ± 0.034	0.395 ± 0.135	0.568 ± 0.000	0.502 —
Texas				
Hudspeth County	0.635 ± 0.079	0.698 ± 0.014	0.722 ± 0.032	0.558 ± 0.022
Mexico				
Ciudad Chihuahua	0.619 —	0.785 —	0.781 —	0.622 —

Some earlier results on diel cycles in lizards are reviewed in a later section of this paper.

In the collections assembled in 1955 there were a number of half-grown and newly-hatched individuals. The results for these groups are separated from the others in Table III to show that there is a distinct effect of age on color-matching, the newly-hatched individuals being least well matched, the adults best, with those of intermediate age between the two extremes. The significance of these results will be discussed in the last section.

The data in Table IV are grouped according to well-defined regions of uniform soil color. Within each of these regions, the soils are considerably less variable from place to place than are the lizards. The changes from one region to another in the colors of both are evident in the independent changes in the reflectances obtained through the various filters.

Such treatment as animals were subjected to prior to being photographed would tend to minimized correlation with soil color by tending to make the entire group more uniform after collection, detention in a collecting bag and photographing, than before. It may be ignored, therefore, as affecting the stated conclusions.

CHANGES OF COLOR UNDER CERTAIN LABORATORY CONDITIONS

Experiment 1. After the collecting season of 1953 some of the captured lizards were kept under otherwise constant conditions on backgrounds of two different colors for several months to see whether they could be induced to change color by such treatment. During the period the animals were housed in the cage shown in Figure 4, essentially a closed box with a floor area 2.5 x 5 ft containing four sheet-metal pens as shown. The box was lighted with four 40-watt tungsten lamps and heated with a thermostatically controlled electric heater-blower. The lights and heater

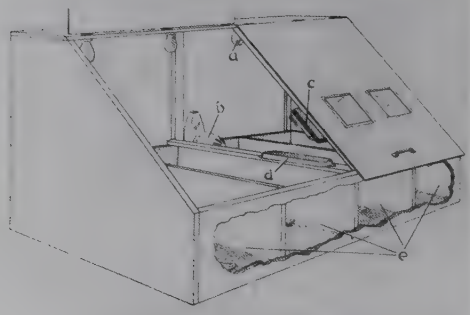

FIG. 4. Holding cage for lizards used in experiment 1. Details are explained in the text.

were turned on at 6:00 A.M. and off at 6:00 P.M. each day. In daytime the temperature was maintained at 31°C; at night it was allowed to fall to that of the room (about 25°). All internal surfaces of the box and pens were painted white. Two of the pens were filled to the same depth, one with white quartz sand, the other with finely ground black cinders. No attempt was made to achieve similar particle-size distributions for these materials; their color-characteristics are given in Table V.

TABLE V. Relative reflectances of earth materials used in the various experiments

Material	No filter	Red	Yellow	Blue
Ground black cinders	0.109	0.164	0.127	0.240
White quartz sand	0.593	0.638	0.639	0.626
Natural red sand	0.365	0.520	0.399	0.384
Natural green sand	0.537	0.504	0.539	0.552

On September 24 two groups of five lizards each were selected randomly from the available material, one placed on the white background, the other on the black. They were fed ants and mealworms, provided with water and otherwise left to themselves until November 12. On this date they were photographed (according to the standard procedure given above), scrubbed lightly with soap, dried and photographed again. They were then switched to backgrounds of opposite color, photographed successively on November 16, November 24, December 10 and December 23, and finally washed, dried and photographed again on December 23. The photographs obtained were handled according to the procedure described above; the reflectance percentages obtained are given in Table VI and compared in the analysis of variance shown in Table VII.

The five individuals making up each of the groups used in this experiment were selected at random from the entire group of lizards surviving to September 24, but they proved to differ somewhat in mean albedo at the beginning of the experiment (Table VII, item 3). This difference is of no consequence in interpreting the remaining results.

There was a pronounced darkening of the lizards that were on a black background until November 12; the effect was greatly reduced by washing and was therefore partly the result of adherence of finely pulverized substratum to the skin. The residual effect was still found to be significant. In this analysis, the two-way interactions between "filters" and other factors measure the tendency of the reflectances through the various filters to change disproportionately and are thus a measure of change of color (chromaticity or saturation) independent of changes in brightness. In this instance, the darkening appeared also to involve a change in color which was again partly but not entirely associated with the material removable by washing. The change, represented by reduced reflectivity at the red end of the spectrum, or a shift in color toward that of the background (see Table V), could be explained either as a change in skin pigmentation or as evidence that the washing did not remove all adhering foreign material from the skin. With respect to the tendency to darken and the change in color, all five individuals behaved similarly; the changes were not simply shifts in the means of the group.

After being on a white background until November 12, the other group of lizards showed no change in mean albedo or in color before or after washing. The small changes in albedo that did occur from one individual to another were both positive and negative. The failure of washing to bring about any change in color or albedo is probably due to the fact that the material used to provide the white background was of uniformly large particle-size and lacked the dust-like fraction of the ground cinders. Any significant desaturation produced through adherence of white material to the skin would have registered in this analysis as a change in color.

Following transfer of the two groups to backgrounds of opposite color, further changes occurred that may be followed in Tables VI and VII. Those lizards originally on a black background did not change in albedo or color upon being transferred to a white background. Changes through December 10 are included in the analysis in Table VII, which shows no significant increase from November 16 to December 10. After De-

TABLE VI. Mean reflectances of specimens of *Phrynosoma modestum** during experiment 1

	No filter	Red	Yellow	Blue	No filter	Red	Yellow	Blue
	Lizards on black background				Lizards on white background			
Field colors	(5) 0.491	0.540	0.580	0.477	(5) 0.432	0.484	0.456	0.421
November 12 (before washing)	(5) 0.227	0.283	0.256	0.323	(5) 0.403	0.435	0.458	0.468
November 12 (after washing)	(5) 0.330	0.361	0.366	0.389	(5) 0.401	0.453	0.466	0.433
	Switched to white background				Switched to black background			
November 16	(5) 0.323	0.385	0.376	0.366	(4) 0.380	0.475	0.448	0.396
November 24	(5) 0.290	0.432	0.361	0.366	(2) 0.268	0.382	0.360	0.350
December 10	(5) 0.313	0.400	0.350	0.379	(2) 0.290	0.392	0.311	0.372
December 23 (before washing)	(3) 0.334	0.408	0.441	0.482	(2) 0.278	0.381	0.383	0.464
December 23 (after washing)	(3) 0.348	0.393	0.449	0.460	(2) 0.378	0.448	0.423	0.444

*Numbers in parentheses are numbers of animals surviving to the date given and the number of values contributing to each mean.

cember 10, a tendency of the lizards to die makes the results unreliable, although albedo apparently increased during that period.

For the lizards transferred from white to black on November 12 the changes corresponded approximately to those found for the lizards originally placed on a black background, but they were of smaller amplitude. Deaths of the animals throughout this period make the results very uncertain.

Experiment 2. Some of the survivors of the collecting season of 1954 were kept for short periods of time under various conditions of temperature, background color and light intensity for further examination of change in individual color or albedo. The tests themselves were carried out in small boxes like the one shown in Figure 5. They were of such size as would fit inside the photographing apparatus after removal of the scaffolding supporting the light, so that lizards inside could be photographed during an experiment without having to be handled or moved from place to place. The testing boxes were lined with cardboard on which colored sand was pasted, and filled to a depth of about 1 cm with the same sand. Four of these boxes were made, with the following linings: white quartz sand, natural red sand, natural green sand and finely ground black cinders. The red and green sands were obtained by crushing and sifting samples from sandstone outcrops in the vicinity of Madison. Reflectance values for the materials are given in Table V.

During tests, the boxes were lighted at various intensities by using separately the fluorescent element or the (25-watt) incandescent bulb shown in the figure over a frosted glass cover (not shown), or were made completely dark by covering with an opaque cover. The resulting light intensities

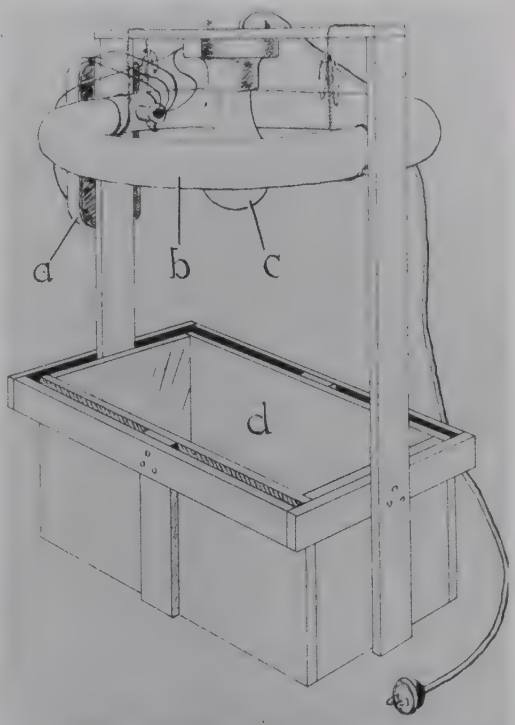

FIG. 5. Testing box used in experiment 2. Scaffolding supporting the light is removable, permitting the box itself to be placed inside photographing apparatus (Fig. 2). In use, the box is covered with frosted glass or an opaque lid (not shown).

inside the box are given in Table VIII. Temperature was varied by keeping the boxes in a cold room at 7°C, in an incubator at 40° or in a room in the center of the building where the temperature varied little from about 25°. Ordinarily a test

TABLE VII. Analysis of variance for experiment 1: effect of background color over a period of several months

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	F
Part I. Comparison of the two experimental groups before treatment				
Total	39	3,155.55		
Filters†	3	363.87		
Experimental groups	1	542.43	542.43	8.02‡
Filters x groups	3	85.29	28.43	0.42
Error	32	2,163.96	67.62	
Part II. Analysis of data for lizards beginning the experiment on the black background				
Total	119	11,136.81		
Filters	3	824.14		
Dates	5	6,633.32		
Dates on white vs. dates on black	1	201.47	201.47	11.87‡
Washed vs. unwashed	1	749.09	749.09	44.14‡
Field reflectance vs. mean reflectance on black	1	5,670.50	5,670.50	207.20‡
Dates on white	2	12.23	6.12	0.36
Individual animals	4	1,175.62	293.90	17.50‡
Filters x dates	15	732.17	48.81	2.88‡
Filters x individual animals	12	233.12	19.43	1.14
Dates x individual animals	20	529.53	26.03	1.54
Error	60	1,017.91	16.97	
Part III. Analysis of data for lizards beginning the experiment on the white background and surviving until December 10				
Total	55	3,356.30		
Filters	3	521.75		
Dates	6	804.54		
Dates on white vs. dates on black	1	415.96	415.96	6.94*
Dates on white	2	116.66	58.33	0.97
Washed vs. unwashed	1	0.72	0.72	0.01
Field reflectance vs. mean reflectance on white	1	115.94	115.94	1.93
Dates on black	3	271.92	90.64	1.51
Individual animals	1	480.29	480.29	8.01*
Filters x dates	18	402.50	22.36	0.37
Filters x individual animals	3	104.82	34.94	0.58
Dates x individual animals	6	923.94	153.99	2.57
Error	18	1,079.04	59.95	

†Including readings taken without filter.
*Significant at the 5-percent level. ‡Significant at the one-percent level.

TABLE VIII. Light intensities (footcandles) inside the various test-boxes and in holding cage

Light source	Lining Material			
	Black cinders	White sand	Red sand	Green sand
Fluorescent element	49.8	53.8	52.5	44.0
Tungsten lamp (25 watts)	14.7	17.4	15.8	14.5
Holding cage	21.8			

was carried out by placing a lizard in one of the test boxes early in the afternon and photographing it along with a standard white surface immediately. The box was then held under a particular combination of light intensity and temperature for 24 hours, the lizard being photographed in the box at the end of the period without being disturbed.

It was originally intended to test each lizard at each combination of light intensity, background color and temperature, but deaths of the animals prevented even near completion of this design. The results obtained are given in Table IX; these are expressed as the difference between the mean of the four reflectance values obtained before the 24-hour period spent under each of the sets of conditions described and the mean of the four reflectance values obtained at the end of the period. Such differences were averaged for all lizards held under identical sets of conditions. These values are measures of change in albedo, but not in color.

In general, the changes in albedo produced by any of the tested combinations of conditions are not significant. The changes themselves are of small magnitude in most instances, and their standard errors are large. There appears to be some evidence that the lizards bleach when they are transferred to the lowest temperature, but the tendency is not consistent. Changes in color were investigated by subjecting particular segments of the data, those in which a reasonably large number of animals had been tested under a given set of conditions, to analysis of variance, the results of which are presented in Table X. In all of the examples given, changes in albedo with temperature are shown by the significant values of F for "temperature." These particular experiments showed bleaching at low temperatures and darkening at high temperatures. There is no evidence in any of the analyses for a change in color with temperature (non-significant values of F for the two-way interaction "filters $\times$ temperature"). *Experiment 3.* Possible effects of one of the collecting techniques were examined by "recapturing" some of the animals in the laboratory, *i.e.* lizards were taken from their holding cage at 9:00 A.M., photographed and confined in a collecting bag until 1:00 P.M. the same day, whereupon they were removed, photographed again and replaced in the cage. During the interval, they were held at about 25°C; no attempt was made to control the temperature accurately. Four lizards were used, each one submitted to the procedure on three separate days. Results are given in Table XI. Comparison of the reflectances before and after treatment shows a significant change in no instance.

Discussion

Several investigators have been able to show that such environmental components as light in-

TABLE IX. Changes of albedo in lizards transferred from holding cage to test-boxes under the various conditions given. Numbers in the table are mean differences between means of four reflectances obtained before and after a 24-hour period under the test conditions

	Fluorescent element		Tungsten lamp		Completely dark		
Back-ground	25°	40°	7°	25°	7°	25°	40°
Black	−0.011±0.030	0.032±0.021	0.062±0.025	0.064±0.040		0.019±0.024	0.011±0.084
White	−0.028±0.049	0.014±0.035	−0.086±0.037	0.016±0.032			−0.013±0.011
Red	0.030±0.033	−0.041±0.029	0.043±0.025	0.014±0.024		−0.018±0.052	
Green	0.005±0.035	0.010±0.030	0.027±0.022	−0.048±0.038	0.095±0.025		

TABLE X. Analysis of variance for experiment 2: effect of temperature on color and albedo

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Squares	*F*
Part I. Lizards on green sand under tungsten lamp, 25° and 7°				
Total	79	8,926.78		
Filters†	3	197.03		
Temperatures	1	1,016.03	1,016.03	10.20‡
Individual animals	9	1,249.23	138.80	1.39
Filters x temperatures	3	399.62	133.21	1.34
Filters x individual animals	27	1,376.13	50.97	0.51
Temperatures x individual animals	9	1,999.13	222.13	2.23
Error	27	2,689.61	99.62	
Part II. Lizards on red sand. under fluorescent light, 40° and 25°				
Total	79	10,442.99		
Filters	3	482.24		
Temperatures	1	881.13	881.13	10.136‡
Individual animals	9	1,798.90	199.88	2.30*
Filters x temperatures	3	101.03	33.68	0.39
Filters x individual animals	27	2,310.00	85.56	0.98
Temperatures x individual animals	9	2,522.53	280.28	3.22‡
Error	27	2,347.16	86.93	
Part III. Lizards on white sand under tungsten lamp, 25° and 7°				
Total	71	8,306.26		
Filters	3	34.66		
Temperatures	1	888.38	888.38	11.60‡
Individual animals	8	1,762.62	220.33	2.88*
Filters x temperatures	3	331.13	110.38	1.44
Filters x individual animals	24	2,703.21	112.63	1.47
Temperatures x individual animals	8	747.53	93.44	1.22
Error	24	1,838.73	76.61	
Part IV. Lizards on black sand under tungsten lamp, 25° and 7°				
Total	87	10,251.38		
Filters	3	240.40		
Temperatures	1	510.25	510.25	6.00*
Individual animals	10	2,941.61	294.16	3.46‡
Filters x temperatures	3	172.30	57.43	0.68
Filters x individual animals	30	2,335.08	77.84	0.92
Temperatures x individual animals	10	1,502.52	150.25	1.77
Error	30	2,549.22	84.97	

†Including readings taken without filter.
*Significant at the 5-percent level. ‡Significant at the one-percent level.

TABLE XI. Relative reflectances of specimens of *Phrynosoma modestum* before and after 4-hour detention in a cloth collecting bag

1. Reflectances at 9:00 a.m. of lizards just removed from holding cage (each value is the mean of 3 determinations made on 3 different days)

Lizard No.	No filter	Red	Yellow	Blue
7	0.316	0.410	0.421	0.447
17	0.272	0.350	0.378	0.433
18	0.331	0.468	0.456	0.515
19	0.324	0.408	0.445	0.422

2. Reflectances at 1:00 p.m. of the same day, immediately after 4 hours in collecting bag (each value is the mean of 3 determinations made on 3 different days)

7	0.345	0.444	0.409	0.483
17	0.383	0.476	0.400	0.482
18	0.364	0.476	0.494	0.484
19	0.437	0.460	0.427	0.501

tensity, light quality, temperature and background color are able to effect changes in the individual albedo for selected species of lizard closely related to *P. modestum*. The available results have generally shown that albedo tends to increase with increasing temperature (Parker, 1906: *Phrynosoma blainvillii;* Redfield, 1918: *P. cornutum;* Atsatt, 1939: *P. platyrhinos*) and to decrease with increasing light intensity (*opera cit.*). They also suggest that there is an interrelation between temperature and light intensity such that light is able to exert its characteristic effect only within an intermediate temperature range (20-30°C: Redfield) but not when the emperature is extremely high or extremely low. The temperature range in which light controls albedo appears to vary from one species to another (Atsatt). There is also evidence for the existence of internally-controlled diel cycles of change in albedo which persist in the absence of environmental changes (Caswell 1950: *Xantusia vigilis*) in which there is a dark phase ordinarily corresponding to the daytime hours and a pale one reaching maximum development early in the evening. Altogether, there seems little reason to doubt that individuals of *P. modestum* are capable of changing albedo in response to various environmental changes. None of the authors cited, with the exception of Atsatt, has investigated changes of color as these could occur independent of changes in albedo, and Atsatts results are unclear because they were obtained by direct visual com-

parison of her specimens with a standard color-chart. We have been unable to find evidence for color-change except in the one instance where the change could be explained as due to the adherence of foreign material to the skin.

Wherever local polychromatism is thought to be the precursor of speciation or to be the evidence of ecological isolation, it is first necessary to be certain that the polychromatism is genetically determined and not the result of locally specific environmental factors acting directly upon individual phenotypes. We have been able to show that there is variation in color among local populations of *P. modestum* and that the locally characteristic colors are related to the colors of the soils on which the populations occur, where the meaning of the term "related" is given by the method used for making the comparison, as explained above. The results of the laboratory investigations provide evidence that individual lizards are not able to change color under a variety of laboratory conditions, although they may change albedo.

This does not yet mean, however, that the polychromatism has any evolutionary significance. The populations of adult lizards that we have studied represent the last result of all selective processes that are able to exert a measurable effect upon the frequencies of various phenotypes over the life-span of an individual, and may be very far from representing the complexion of the entire antecedent population of eggs or hatchlings. It is very interesting that the correlation between skin-color and soil-color tends to increase with age and is practically nonexistent in very young and half-grown animals, suggesting that the color of hatchlings is indifferent to background and that an apparent correlation later appears as a result of differential mortality, or alternatively that the color of the individual's skin is in fact plastic but to such a slight degree that a considerable fraction of the lifespan has passed before a noticeable convergence to the soil-color has occurred.

We have also shown that one of the components of matching coloration or albedo may be simply the accumulation on the skin surface of finely pulverized substratum, and we cannot be certain that this has not contributed to the correlation found in the field, where only unwashed animals were examined.

Considering all the foregoing possibilities, one must concluded that there is no decisive evidence for the existence of ecological races in *P. modestum*. The correlation in the field of adult animals with their backgrounds is a fact, and it is unlikely that this correlation can result from the momentary action of the pigmentary effectors. On the other hand, that it is the result of genetic segregation within a series of ecological races is only one of a series of alternative explanations, the others of which cannot be eliminated at this time.

Summary

This paper describes a study of color in the round-tailed horned lizard, *Phrynosoma modestum* Girard. The species is a small, uniformly colored, sedentary animal inhabiting the North American shrubby desert. An attempt has been made to demonstrate that the dorsal color in local populations of the lizard tends to match the color of the local soil, and to interpret the matching in terms of the ability of the animals to change color under laboratory conditions.

Colors of lizards and soils are described by means of an arbitrary three-primary system. Photographs of the specimens were taken under standard (Geissler Tube) illumination through three filters of known transmission characteristics. The intensity of illumination reflected from the specimens through each filter was computed after measuring the density of the developed image spectrophotometrically, and then expressed as a fraction of the intensity reflected from a standard white surface through the same filter. A short discussion is included of the errors inherent in such a method of color measurement.

Significant correlations were found between intensity of reflection, through all filters, from the backs of adult lizards and from the soils on which they were collected. Correlations were weak or nonexistent for half-grown or newly-hatched individuals. Lizards kept on backgrounds of ground black cinders or white sand for periods of several weeks showed strong changes in albedo and weaker changes in color, which could at least in part be explained as resulting from adherence of substrate material to the skin. It was not possible to demonstrate that lizards are able to change color over periods of 24 hours when subjected to various changes in temperature, light intensity or background color, although some combinations of the various levels of these variables were able to produce changes in albedo. The latter were most obviously related to changes in temperature, cold usually being followed by bleaching. Much variation in the behavior of individual lizards made it impossible to find consistent responses over short periods to changes in light intensity or background color.

Although the color variation found in the field was generally greater than that producible in the laboratory, the failure of correlation among

younger animals and the possibility that matching coloration is at least partly the result of adherent substratum material makes it impossible to conclude that the distinctly colored populations represent incipient ecological subspecies, or even that the local color-correlation is the result of genetic differences among the local populations.

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THE CORRELATION OF COLORATION WITH SOCIAL RANK IN *GAMBUSIA HURTADOI*[1]

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Correlation of coloration with aggressive behavior and social relationship in fishes has been mentioned by several authors (Braddock 1949, Breder 1948, 1949, Collias 1944, Noble 1938). Experiments designed specifically to observe coloration changes among individuals in a social hierarchy have seldom been reported. In this work a group of 39 laboratory reared *Gambusia hurtadoi* was variously divided into separate aquaria, and individuals were transferred from one group to another as social relations were established. The coloration of fishes of different social rank was noted during 70 days of observation.

Methods and Materials

Gambusia hurtadoi was described by Hubbs and Springer (1957), who considered it to belong to the *Gambusia nobilis* species group. In addition to meristic characters it can usually be recognized by a broad, dark lateral band overlaid with darker crescents. The venter of living specimens is an iridescent blue. At present this form has been recorded from a single spring system in the state of Chihuahua, Mexico, and its distribution is apparently allopatric to that of other members of the species group. A description of *G. hurtadoi* and notes on its variability, ecology, and evolution are given by Hubbs and Springer.

All individuals used in this experiment had been kept together in a 45 gallon aquarium for several months prior to the observation period. Five experimental tanks of two sizes were used. Tanks 1 and 2 were 90 × 60 × 30 cm and tanks 3-5 were 60 × 30 × 30 cm in size. These aquaria were unequally separated from each other, and 1 and 3 were exposed to brief intervals of late afternoon sunlight. Because of vegetation, tanks 1 and 2 were somewhat darker than the other three. About midway through the experiment an opaque shield was placed behind tank 3 so the colors of the fishes could be better observed. When a fish was isolated, the sides of its tank were shielded

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so that fishes in adjacent aquaria could not be seen from within the tank. Temperature and food were approximately equal among the tanks.

During sexual activity the behavior of *G. hurtadoi* is such that in any social hierarchy, the female plays a neutral role. All nip-right and nip-dominance activities occur among the males. Territoriality is not known to be characteristic of the species, and dominance relations originate through male rivalry for the females. During the experiments the males spent almost all of their time following females, and the degree of vigor exhibited varied with the individual.

In ideal cases a higher social rank was indicated by a greater amount of yellow in a male's dorsal fin, at the base of the caudal fin, and on the ventral portion of the caudal peduncle. Tank dominants had deep yellow dorsal fins and sometimes an additional yellow tinge along the dorsolateral region as well as a deepening of the black border along the outer edge of the dorsal fin. When a social hierarchy had become stabilized in any aquarium the dominant fish could be picked out by color alone. Coloration of subordinates was not always directly related to their social rank. Dominant males in the related species *G. heterochir* can be recognized by increased color intensity, in this instance black (Warburton, *et al.*, 1957).

Results

Dominance in a Newly-formed Group

A group of four equally-colored males and four females was introduced into tank 3. On the same day, several hours after being moved, one fish (L) was yellower than the others, and it drove all other males, especially male G. Three days later L definitely dominated two males (R and G) but was often rebuffed by the remaining male (D). At this time the fishes were classified as to intensity of yellow $L = D > R > G$. Nine days after being put into tank 3, L was undisputed dominant. A day later a reversal was noted among the subordinates for R had gained dominance over D. The fishes could be classified both as to social rank and yellow intensity $L > R > D > G$. No true fighting was observed, and L was the smallest but most aggressive male of the group.

Effect of Dominant Removal upon the Group

L was removed from the group. About 12 hours later R was noticeably more active in the tank than he had been while L was present. R seemed especially aggressive toward D. At this time there was only a very slight difference in yellow intensity between these two fish, and neither exhibited the deep dorsal fin yellow that L had attained. For the next week R dominated the tank, but D paralleled him very closely in color. Eight days after *L's* removal R was definitely more yellow than D, and he became very belligerent, chasing D and G quite vigorously. Two days later D actually seemed to be the most yellow male, but this soon reversed again and the relations stabilized with the males categorized in social rank and yellow intensity $R > D > G$. It was noted during this experiment that the amount of yellow exhibited by an individual male often varied with his emotional state. Twice a male was observed to change his color (once to pale; once to increase the amount of yellow) upon the approach of an observer to the tank. This may account for the variation of yellow in D when his social rank was apparently unaltered.

Effect of Return of Original Dominant to the Group

Sixteen days after his removal, L was returned to the group in tank 3. On the same day G was removed, since he was the omega (lowest ranked socially) fish and was not expected to contribute anything further to the social hierarchy. At this time the important role of the omega was not realized. Greenberg (1947) has pointed out that the omega fish serves as a tension-release for higher-ranked individuals, and it is more often chased than any other fish. Removal of the omega may increase the frequency of drives on other subordinates.

Both R and D were more yellow than L when the latter was returned to the tank. Soon after L's introduction he and R were observed in a threat display. The fish swam after each other in a circle. The dorsal fins were raised and the fish alertly eyed each other. Neither was victorious but both were observed to chase D. By the following day L had gained his old dominant color and R had attained the same yellow intensity. For two days this situation continued, with neither R nor L a true dominant. Six days after his return to the group L was definitely termed the dominant fish. All three males seemed to have lost some of their yellow intensity, and L was chiefly distinguished by having more dorsal fin yellow. The group was considered stabilized and the males classified as to social rank $L > R > D$ and in degree of yellow $L > R = D$.

Effect of Introduction of a Foreign Male into a Group

A large male (Z) was introduced into the group of three males (L, R, and D) and four females. Prior to being moved, Z had deep yellow in both dorsal and caudal fins. When dropped into tank 3, the foreign male showed fright pallor and when

he regained his normal coloration the yellow in the fins was lacking. Although no fighting was observed, *L* soon seemed to gain a much more intense yellow in his fins and posterior body. During the next day *L* remained very yellow and *Z* had only a yellow tinge at the base of the caudal fin. *D* and *R* were about identical in color, and both were more yellow than *Z*. On the second day after *Z*'s introduction *L* was observed to make repeated vigorous drives on *Z*, and the latter offered no resistance. The rank of the three subordinates was not clear, for *Z* was observed to make one drive on *D* and one on *R* without being rebuffed by either. Three days after the introduction of the foreign male the fish were classified in social rank $L > R = D = Z$. According to intensity of yellow the fish were $L > R = D > Z$

Braddock (1949) has mentioned that in *Xiphophorus maculatus* the effect of prior residence gives a resident male a decided advantage over an intruder, and that this factor may delay the social rise of a superior individual. This very likely applies in the present case, for *Z* had at one time been a dominant and he was larger than *L*. At the close of the experiment *Z* was apparently gaining in dominance over the other two subordinates and he might soon have challenged *L*. Upon the introduction of a foreign male in this experiment, then, the dominant male intensified in yellow and at least temporarily relegated the intruder to omega rank, with a consequent loss of yellow in the latter.

Effect of Isolation upon the Coloration of a Group Dominant

Three dominant males (*L*, *Y*, and *R*) were isolated for intervals of four to six days. All these fish retained their vivid yellow fins and posterior body colors. One male (*L*) was isolated from other males and placed with a series of four females in tank 4. His dominant coloration paled slightly during ten days of observation. Males *X*, *Y*, and *Z* were isolated from females and kept together in tank 1 for 16 days, during which they all remained yellow. In this case a weak dominance was set up $Y > Z > X$, but the fish were very similar in the amount of yellow exhibited. It seems that once a dominant fish gains his distinctive color, only a defeat from a rival male causes him to lose it. An exception to this is a state of extreme emotion, as when fright pallor is induced, but this is only temporary.

Fighting and Threatening as Color Stimulants

Fighting or threatening always induced a maximum amount of yellow in the fins and posterior body and resulted in a more intense black border on the dorsal fin of male fish. An example of this occurred in tank 4 where the males were classified $G > N > S$ in both rank and color. There were three females present. *G* was removed for 48 hours, during which time *N* dominated *S*, but the former did not gain the degree of yellow usually shown by a tank dominant. *G* was returned to the tank and about 30-45 seconds later he had lost his fright pallor and regained his intense fin yellow. *N* at the time of *G*'s return, was not particularly yellow. Five minutes after *G* was introduced, he and *N* were swimming about in a tight circle giving each other nips in the predorsal area and engaging in very vigorous body contact. Both *N* and *G* were at their maximum yellow intensity and the black margins of their dorsals stood out conspicuously. The dorsal fins were held rigidly erect. Five to seven minutes after the two stopped fighting, *G* exhibited his victory by chasing *N* with no resistance from the latter. At this time *G* had bright yellow fins and *N* had paled until only a yellow tinge was present at the base of the caudal fin.

Change of Color in an Omega Fish with Rise in Social Rank

During the first 39 days of observation one male (*G*) had been an omega fish. He was chased most frequently by his superiors and had least contact with the females. He had consequently never shown more than a trace of yellow in the dorsal and caudal fins. *G* was placed in tank 4 with three females, but in three days he failed to gain more than a trace of yellow at the base of the caudal fin. A small, very active male (*S*) was introduced and *G* immediately yellowed and began to dominate this fish. For two days following *S*'s introduction *G* continued to dominate, but he paled until the yellow in his dorsal and caudal fins was inconspicuous. Six days after *G* had been put with the females another small male, *N*, was introduced. *G* almost immediately exhibited intense yellow in his fins and became active in "shouldering" *N* away from the females. The introduction of *N* apparently stimulated *G* into a true dominant coloration, for two days later the group had stabilized with the males $G > N > S$. *G* was intense yellow in both dorsal and caudal fins and on the ventral surface of the caudal peduncle. The smallest male, *S*, exhibited no yellow.

Dominance and Coloration Relations in a Large Tank

Seven males and 19 females were placed in tank 2. During the first week a tank dominant (*Y*, the largest male present) and two close rivals (*X* and *Z*) were noted. All other males lacked the yellow

exhibited by these three fish. *Y* was especially conspicuous because the black margin of his dorsal fin was very intense. Thirteen days after the group was formed, *X*, *Y*, and *Z* were removed, leaving five pale subordinate males and 15 females (one other small male had been added to the group and four females had been transferred to another aquarium). On the next day the largest of the remaining males (*Q*) had attained considerable yellow in his fins and during the following 19 days he was tank dominant. Male *Z* was returned to the group twenty days after the removal of *X*, *Y*, and *Z*. Immediately he and *Q* engaged in a vigorous fight which *Z* won. Thereafter *Q* and *Z* both remained in full dominant coloration, each driving all other males, and *Q* keeping well away from *Z*. The tank was large enough for *Q* to be dominant as long as he avoided *Z*. The group stabilized in this manner and no other males developed yellow coloration. In none of the smaller aquaria did a group stabilize with two fish simultaneously in dominant coloration.

A group of four males (*L*, *R*, *D*, and *G*) and four females was introduced into tank 2 and observed for 12 days. This is the only instance in which a social hierarchy was not set up, presumably because of the large area available for scattering of individuals. This series was later placed in a small aquarium and a social hierarchy was established. The males were classified in coloration and social rank $R > L > D > G$. The fish were then returned to a large tank where *R* apparently tried to continue his dominance. After three days in the large aquarium males *L* and *D* had increased in yellow intensity and both were active with the females. Only *G* remained pale and stayed by himself. Male *R* was still the dominant fish, but he was unable to prevent *L* and *D* from chasing the females. It is evident that a small area is necessary for social hierarchy to develop, and this system is weakened when the individuals can be relatively dispersed.

Before the fish used in these experiments were divided into various aquaria, all 39 individuals occupied tank 1. Here could be seen individual males which frequently drove other males, but no tank dominant was noted; nor did any fish exhibit noticeably more yellow than the others. Collias (1944) has mentioned that as the size of a group increases it soon passes the threshold of individual recognition and strangers are usually freely admitted into the group. This apparently was true in tank 1.

Coloration of Socially Closely-matched Males

In tank 4 a rather complicated series of rank reversals accompanied by coloration changes was noted among males *L*, *D*, and *N* in the presence of three females. In previous experiments *L* had dominated *D*. The other male (*N*) had not been with *L* and *D* in experiments. *N* was placed with the females for two days, during which time he gained only a slight tinge of yellow at the base of the caudal fin. *D* was introduced into the group and in little more than three minutes *N* had noticeably yellowed and was seen to drive the foreign male several times, and to actively shoulder him away from the females. Two days later *D*'s superior size seemed to overcome the aggressive behavior of *N*, for *D* had gained a very vivid yellow in the dorsal and caudal fins and a conspicuous black dorsal fin border. Three days after *D*'s introduction, the final male, *L*, was put into the tank. Within the first few minutes after his introduction *L* exhibited his dominance over *N* by driving the latter several times. *D* and *L* soon began feinting and threatening each other as they swam in a tight circle. *D* was in full dominant color, but *L* seemed to have only incompletely regained a normal coloration from his fright pallor. After threatening *L* with no decided victory, *D* sought out *N* and drove him. *L* soon gained a dominant coloration and between his brief encounters with *D* he chased *N*. The latter fish, however, finally began to rebuff *L*, and some time later *N* gained noticeable yellow in his fins, and upon provocation he was seen to actively drive *L* several times. One half hour after *L*'s introduction *N* seemed to have gained dominance over *L*, although both *L* and *D* were more yellow than *N*. During the following four days, all three males gained and retained full dominant coloration. Both *L* and *N* were small, aggressive fish while *D* was a large, less active one. Quite suddenly on the fifth day after *L*'s introduction, the fishes were observed to vary in yellow intensity $D > N > L$, with *L* exhibiting almost no yellow. Observation showed that this classification reflected the social status. *N* was especially vigorous in his dominance over *L*, but he was definitely subordinate to *D*.

Other Observations on Social Relationships

Several observations of interest were incidentally made during the course of experimentation. It was found that a subordinate fish from group *A* could be placed into group *B* and there become a dominant. If then the dominant from group *A* were introduced into *B*, he occasionally could not achieve dominance over his one-time subordinate. This is apparently a result of prior residence or "having become accustomed to dominate" on the part of the one-time subordinate. This relation-

ship was noted in tank 4 when *L* was unable to dominate *D*, although he had done so in tank 3.

The importance of the omega fish, mentioned above, was seen once during the period of observation. A group recently placed into tank 3 was just establishing a hierarchy in which male *R* was gaining dominance over another male (*L*) which had long been a tank dominant. Each time *R* drove *L*, the latter sought out the omega fish (*G*) and vigorously chased him. This sequence of events was repeated many times, being initiated by *R* and terminating with *G* being chased by *L*.

The tank dominant often was the largest male. However, some of the most conspicuous dominant fish were small, and they always exhibited very aggressive behavior and great vigor in chasing females. These small dominants seemed to have a paler ground color than larger, less active ones. An outstanding example of the small aggressive dominant was *L*, which at one time or another at least temporarily dominated practically every other male in the series.

Discussion

The selective value of the social hierarchies observed can be theorized. The dominant fish exhibited his rank in one major way—by attending any female he selected, and usually by keeping other males away from the females. The larger the area, the more difficult this latter task became. In many instances (although not observed in these experiments with well fed fish) the dominant of a group may also exhibit his superiority in such ways as by obtaining the most select morsels of food and the best habitat niche in the area. Since the dominant is the male most likely to leave offspring, this would lead to an integration of his characteristics into most future generations in the group. It would not necessarily lead to a progressively more belligerent population, since presumably a whole series of factors must control complex characters like aggressive behavior and dominance. In nature, where the subordinates are free to leave a group in which they are vigorously driven by a dominant, the above principles may not be so simply applied.

The actual role of the coloration of males of various social rank is hard to determine. That it helps subordinates to recognize the dominant and serves as a warning of his approach is probable. However, the movements and overall behavior of a group dominant would probably achieve the same result. The fact that the dominant almost continually holds his dorsal fin erect while subordinates do so only when approaching a female or when challenging another male may be of some significance. The vivid black-bordered yellow dorsal fin of the dominant fish very likely serves as some sort of an indicator.

In one experiment there were many females and a few males (including a tank dominant) in tank 2. Into this tank a non-yellow male was introduced. The dominant fish took no notice of the foreign male during a 15 minute interval. It was also noted that the intruder did not try to avoid the dominant, and therefore apparently did not associate the dominant's coloration with superior rank. A dominant- colored male was introduced into the group for 15 minutes. The resident dominant swam past the newcomer several times before a challenge occurred between the two, and this resulted only when the foreign male refused to leave the females. Apparently the sight of a vivid dominant color in a male did not excite the resident dominant fish.

Female selection of the brightest-colored male probably does not function in this species. Males were often observed to approach females from behind and suddenly dart forward to thrust the gonapodium. Warburton, *et al.* (1957) mentioned that copulation in this form is similar to that described by Clark, Aronson, and Gordon (1954) for *Xiphophorus maculatus* and *X. helleri*, in which females apparently do not select their mates. Probably Noble's (1938) suggestion that in certain cases coloration may merely serve to emphasize gestures and movements comes closest to the actual function of coloration in the species under consideration.

Summary

A series of 39 *Gambusia hurtadoi* was divided into several subgroups, and as social hierarchies became established the coloration of individual males of varying social rank was noted. A tank dominant could be recognized by the presence of bright yellow in the dorsal fin, base of the caudal fin, and ventral portion of the caudal peduncle. The black outer border of the dorsal fin was also more conspicuous. In a simple hierarchy, a fairly rigid nip dominance was set up among the males, and a higher social rank was reflected by a more intense yellow in the dorsal and caudal fins. When the dominant was removed from the group, another fish soon took over the dominance and its coloration intensified accordingly. The introduction of a foreign male into the group caused the group dominant's yellow color to intensify. The intruder usually was relegated to the omega position with a consequent loss of yellow in the fins. The coloration of dominant males tended to remain unchanged during periods of isolation from other individuals of the species. Fighting and threatening always caused an intensification of

yellow coloration and of the black border of the dorsal fin of males. An omega fish could gain a dominant coloration when placed in a group which it could dominate. Available space is an important factor in determining the rigidness of a hierarchial system. The dominant of a small group in a large space could not maintain dominance over his subordinates, and the latter were not as drab as were those in a smaller space. Too many individuals in a small space apparently passed the threshold of individual recognition and a group dominant did not emerge. In one large group in a large space two dominants occurred. The dominant probably fathers most of the offspring of the group. In *Gambusia hurtadoi*, the distinctive coloration of a superior individual probably serves merely to emphasize his movements and gestures toward rival and subordinate males.

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SELECTIVE PREDATION OF GLAUCOUS-WINGED GULLS UPON ADULT RED SALMON[1]

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Introduction

Several authors have reported experimental studies in which selective predation was observed. Such selection has been found based on prey coloration (for example, Cott 1940, Dice 1947, DiCesnola 1904, Isely 1938, Popham 1941, 1942, 1944, 1949, and Sumner 1934, 1935a, and 1935b), upon physical disability of the prey (Mossman 1955, Popham 1942, Ricker 1949, Vibert 1953), and upon age and sex of the prey (Mossman 1955). Van Dobben (1952) reported evidence of selective predation that had nearly experimental accuracy and was obtained under natural conditions. This selection was correlated with physical disability of the prey.

[1] The field work for this study was conducted by the Alaska Department of Fish and Game and supported by Saltonstall-Kennedy funds under Contract No. 14-19-008-2382 entered into with the U. S. Fish and Wildlife Service. The cooperation and assistance of Fisheries Research Institute personnel is gratefully acknowledged. James W. Brooks and Oliver P. Pearson read the manuscript and offered many helpful suggestions. Preparation of this paper has been financed by the Alaska Department of Fish and Game at Juneau and this article constitutes a research contribution of that Department.

In nature, it is seldom possible to obtain observations of predation that approximate in accuracy and number those obtainable under experimental conditions. To my knowledge, such observations in which a differential mortality is correlated with the sex of the prey have not been published. Since an important hiatus in our knowledge of predator-prey relationships can be exposed and partially filled by the observations upon which this paper is based, it is considered reasonable to publish these data in spite of their circumstantial nature.

Methods

This study was carried out during July 1955 on two creeks tributary to Lake Aleknagik, the lowest lake in the Wood River Lake system of Bristol Bay, Alaska. The statistical methods used may be found in Dice (1947 and 1949) and Mossman (1955). The fish were sexed visually and counted using a mechanical tally while walking quietly along the streams. Striking sexual differences in shape and coloration make it entirely feasible to sex red salmon (*Oncorhynchus nerka*) visually in these small, clear and shallow spawning

streams. No jacks (precocious males) were observed during the observations reported here. The male red salmon, when no jacks are present, are, on the average, slightly larger than the females. All salmon carcasses were carefully examined. The red salmon was the only species of salmon present.

Figure 1 illustrates a typical gull-killed female red salmon. The entire act of killing I have not observed personally, but all eye-witness accounts seem to agree that the eyes are picked out first (Mathisen 1955). The salmon seem to become vulnerable to the gulls only in waters of a depth no greater than just enough to cover their lateral lines. After the salmon is killed, and perhaps during the process, the gulls usually drag it into very shallow water or out onto a bar or the shore.

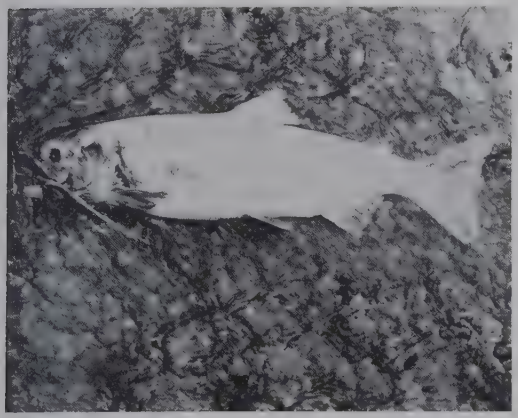

FIG. 1. Adult female red salmon, *Oncorhynchus nerka*, probably killed by gulls. Note that the eye has been removed and that the body cavity has been opened by making a hole just dorsal to the pectoral fin.

In Alaska, almost all salmon carcasses found in shallow water, no matter what the actual cause of death, have at least the upper eye removed by gulls. For this reason, a salmon carcass with a missing eye is not necessarily the result of killing by gulls. Bear-killed salmon usually show the marks of the bear's canines in the back, and frequently the top of the head is also missing as in Figure 2, a photograph of two pink salmon (*O. gorbuscha*) killed by bears.

The identification of a salmon carcass as a gull-kill usually involves the following points: (1) Eye or eyes missing; (2) No sign of any other causes of mortality such as the presence of other possible predators; (3) History of the salmon run indicates that little or no death from "natural" causes could have taken place, or the fish in question is in such physical condition (firmness of belly, lack of scars or fungus, shape, color, condition of eggs if present, etc.) that it is unlikely to have died of "natural" causes. (There is a certain small chance of error here in spite of all precautions known to the author); (4) The body cavity of red salmon if opened by a glaucous-winged gull (*Larus glaucescens*) is entered by a hole made just posterior to the cleithrum, dorsal to the pectoral fin (Fig. 1) or through a hole made just mediad of the cleithrum behind the gills. Frequently the operculum must be lifted in order to see this latter hole. (Pink salmon are usually opened by a hole made near the vent.)

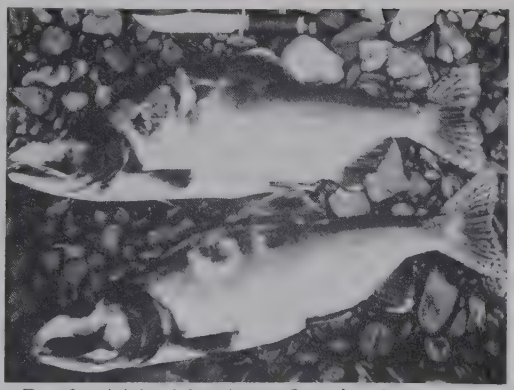

FIG. 2. Adult pink salmon, *Oncorhynchus gorbuscha*, killed by a bear. Note the marks of the bear's canines in their backs and that the tops of their heads have been bitten off. The knife's blade is 5 15/16 inches long from hilt to tip.

Hansen's Creek is a small clear, shallow stream with light-colored, gravel bottom. Salmon carcasses were found throughout the length of the creek until fairly deep water was encountered in beaver ponds at the headwaters. Although there were many fish in this deeper water, and the bottoms of the ponds were clearly visible, no carcasses were found despite a careful search. Carcasses in the stream below were common enough so that usually the next carcass was visible from the one being examined.

Glaucous-winged gulls were abundant along the stream and were the only gull species encountered there. Accurate counts of the gulls, unfortunately, could not be obtained. Since no bear sign was encountered and only one bald eagle (*Haliaeetus leucocephalus*) was seen, it is felt that there was little chance for confusion of gull-killed salmon with those killed by other predators.

The Fisheries Research Institute maintained a man on Hansen's Creek constantly just before and during the spawning run. He reported that the first salmon entered Hansen's Creek on July 21. The period between the first entry of salmon, July 21, and the date of my observations, July 26,

is too short to account for more than a very small number of "natural" deaths. Furthermore, if a great number of natural deaths had occurred, carcasses should have been observed in the beaver ponds where they would have been out of reach of gulls and eagles because of the water depth.

Since no evidence of kills by bears, eagles, or other known salmon predators was found among the fish sampled, and since evidence of gull predation was widespread, it will be assumed that gulls killed all of the fish recorded below.

Findings

Selective Predation

Observations on Hansen's Creek were made on July 26. A complete count on July 25, the evening before these gull-predation observations were made, showed 2,081 live salmon (personal communication).

Of 81 salmon believed to have been killed by the glaucous-winged gulls, 65 were females. At the time this study was made, male salmon in the creek outnumbered females approximately three to one (personal communication, Fisheries Research Institute personnel). The sex ratio prior to this study, during the first days of the salmon run into Hansen's Creek, probably was even more heavily unbalanced toward males. Furthermore, the number of fish in the stream was increasing during this period. It is a characteristic of the χ^2 test of significance that if with everything else remaining constant, we allow the total number of animals (n) to increase, the value of χ^2 decreases. In other words, with an increasing population (n) of fish in Hansen's Creek, when we use the final population count for (n) in our calculations, we automatically increase the conservatism of the χ^2 test of significance as applied to these data. Also, as each fish was taken, it unbalanced the population slightly, making it more likely that one of the other kind would be taken next. This also increases the conservatism of the Chi-square test as used here.

In these calculations, a one to one sex ratio was used to ensure additional conservatism. Using the total population figure of 2,162 (2081 + 81), the adjusted χ^2 was 29.552. Based on the hypothesis that the gulls should kill the two sexes of red salmon in proportion to their numbers in a stream, such highly selective killing of female salmon by the gulls was not to be expected as a result of chance alone. In fact, with this test, any value of χ^2 greater than 6.635 indicates statistical significance at the one percent level. The very conservative selection index, a measure of the intensity of selection (Dice; Mossman, *loc. cit.*), calculated from these data is +.60. (The selection index has a range of −1 to +1, the sign being merely an arbitrary indication of the population receiving the most or least predation as the case may be. To my knowledge, a method for establishing the confidence limits of the selection index has yet to be developed.)

Peaceful Creek (Fig. 3) is similar to Hansen's Creek, but is farther from salt water and the salmon seem to enter it slightly later than they do Hansen's Creek. It is somewhat deeper than Hansen's Creek, and the upper reaches run through a very thick growth of alder. It was studied on July 29, 1955.

Fig. 3. Peaceful Creek, a salmon spawning stream tributary to Lake Aleknagik, the lowest lake in the Wood River Lake system of Bristol Bay, Alaska. The dead salmon is the same one shown in Figure 1. The splashes made by three salmon ascending the stream can be seen; it is in such shallow waters that they become vulnerable to gulls.

Sample sex ratio counts (Table I) allowed calculation of the approximate number of each sex in the total of 426 live fish found in the creek between the lower reaches and the headwaters. This included almost all the water where gulls could attack the salmon. It is felt that this sex ratio of about 189 males per 100 females is sufficiently accurate to be used as it stands.

Fifteen red salmon, believed to have been killed by gulls, were found on the creek. Twelve of these were females. For use in the Chi-square calculations, the number of salmon of each sex was cal-

TABLE I. Sex ratio counts of live red salmon in Peaceful Creek

Count	Females	Males
1	55	102
2	7	12
3	12	29
4	7	9
5	2	6
6	2	7
7	19	30
8	10	20
Totals	114	215

Total different fish in sex-ratio counts..... 329
Total live fish in creek.... 426
Total fish killed by gulls..... 15
Total fish available for predation..... 441

culated utilizing the sample sex ratios given in Table I. The adjusted Chi-square, again with one degree of freedom, was 10.988. The selection index calculated from these data is +.75. Here also, the female salmon suffered significantly heavier predation than the males.

Differential Treatment of Salmon Kills

A further set of observations was made that bears on this problem. The presence or absence of gull-made holes into the body cavity was recorded for salmon carcasses intact enough to be certain of this condition. Pooling these observations for both Hansen's and Peaceful Creeks, it was found that of seven males, four had been opened, while all of 31 females had been opened. These data yield an adjusted Chi-square of 9.133 with one degree of freedom, indicating that there was an unexpectedly strong difference in the treatment the gulls gave the two sexes of fish after killing them.

A possible explanation of these observations would be that in the case of the three unopened male fish, the gulls had been frightened away before they could make the holes. It is highly unlikely that this would occur three times with only seven individuals involved and not once when 31 individuals were involved. Furthermore, the gulls had had time to eat the gills out of one of the uneviscerated males and the gills are by no means always eaten even in fish from which the viscera have been removed. Also, of those males that had been opened, only one was completely cleaned out. The others had all, half, and one-fourth of the milt still intact. Only one of 29 females (Fig. 4) probably contained completely intact viscera (Omissions in the notes make it possible that two of the 31 may not have been cut open to determine this).

DISCUSSION

It appears that the glaucous-winged gulls selectively kill these salmon ultimately because of a difference in the viscera of the two sexes. It is probably the gonads that constitute this difference. (Feeding experiments might help elucidate this problem.) If this suggestion is correct, two problems immediately demand explanation: (1) What are the mechanisms that enable a gull to kill the proper sex so large a percentage of the time? (2) Why and how have these polygamous salmon been able to maintain a strong sexual dimorphism in the face of such stringent selection?

FIG. 4. Adult female red salmon, *Oncorhynchus nerka*, probably killed by gulls. Among the gull kills, uneviscerated females such as this one are seldom encountered. The tally counter is approximately 1¾ inches in greatest diameter.

Since the tendency to return to the home stream is strong in Pacific salmon (for example Chapman 1941, Foerster 1936, Wisby and Hasler 1954), any genetic effects of this selective predation must be diluted very little by fish coming from populations not subject to such predation.

The gulls' "choice" of the salmon to kill may be based upon either learned or innate behavior. The former cannot be discarded off-hand, and in fact might function as an adjunct to innate behavior, but in the face of the extensive behavioral studies on the quite closely related herring gulls (*L. argentatus*), (for example Tinbergen 1951, 1953) it seems an unlikely answer. If the selective predation considered here is a result of innate behavior, many problems arise, including not only the mechanics of such behavior in Alaska glaucous-winged gulls, but also its geographic distribution in this wide-ranging species.

Perhaps this behavior is cued by sign stimuli possessed by females (or individuals desirable from the gulls' point of view) of many species of fish. If this is true, we then probably have at least a partial answer to our second question. (But, in fact, the following argument obtains no matter whether the selection is based on innate or learned behavior.) That is to say, the strong sexual dimorphism shown by these red salmon is not really influenced by this selection. Instead,

the dimorphic character of characters that are learned, or have sign stimulus powers and that result in this selective predation by these gulls are characters that cannot be dispensed with by the female fish and, in addition, cannot now, in the face if this strong selection, be attained by the male. If this is not the answer, then there must be a very strong selective advantage conferred by the red salmon's sexual dimorphism in these particular creeks.

Summary

Glaucous-winged gulls killed proportionately many more female than male red salmon in two spawning streams in Alaska. In addition, the gulls were much more likely to eviscerate the females than the males. The mechanisms that may enable gulls to selectively kill the females, and those that may permit the salmon to maintain strong sexual dimorphism in the face of such stringent selection, are discussed. The tentative conclusion reached is that the characters of the salmon that result in this selective predation are ones that cannot be dispensed with by the female salmon and cannot now, in the face of this strong selection, be attained by the male.

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THE NUMERICAL RESPONSE OF AVIAN AND MAMMALIAN PREDATORS DURING A GRADATION OF THE SPRUCE BUDWORM[1]

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Introduction

It seems to be rather generally agreed that the most effective species of predators affecting an animal population are likely to be those that show a response to changes in its density. Such a response can take either or both of two forms. The population density of the predators may change as a result of changes in prey density, and this Solomon (1949) has aptly termed the "numerical" response. The present study shows that some species of predators increase when prey density increases while others decrease; thus it is necessary to distinguish between a direct numerical response and an inverse numerical response. The numerical response to prey density is more likely to be a delayed than an immediate response. Varley (1953) has already pointed out that the term "delayed density dependence" is more appropriate than "density dependence," because the correlation coefficient between predator and prey populations may be approximately zero when there is a direct but delayed response. The second type of response, or "functional" response, is concerned with food habits. When one species of prey becomes abundant, the predator may respond to the increased availability of this species by concentrating its searching activities upon it. Curves showing both the numerical and the functional response can be combined to give the total response.

In studies on the spruce budworm, *Choristoneura fumiferana* (Clem.) on the Green River Watershed in northern New Brunswick we are attempting to express both of these responses quantitatively over a long period of years. This is but one aspect of a broader investigation on the population dynamics of the insect, the approach to which has already been outlined (Morris and Miller 1954; Morris 1957). Considerations of time and space make it necessary to limit the present paper to avian and mammalian predators, and to deal only with their numerical response. The field data were gathered during the 10-year period 1947-1956. Results will be presented in more detail at a later date and will include the functional and total responses.

Those who may be interested in the subspecific identities of the birds and mammals listed here are referred to Squires (1952) for the birds of New Brunswick and Morris (1948) for the mammals.

Materials and Methods

These studies are being conducted in a section of the boreal forest of Canada. On a series of permanent ecological plots, varying in size between 20 and 25 acres, the population of the spruce budworm and associated defoliators has been measured since 1945. The populations of small birds and mammals have been measured on the same plots since 1947. A diagrammatic representation of one plot is presented in Figure 1.

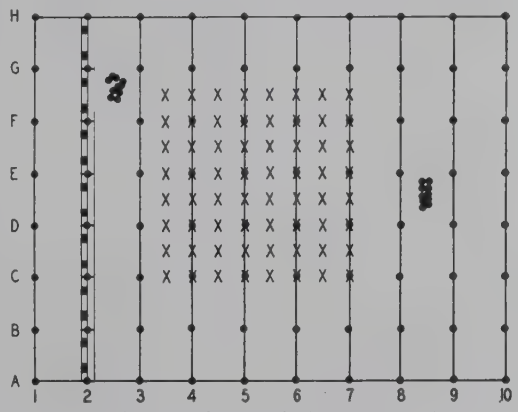

Fig. 1. Diagram of an ecological plot on the Green River Watershed. The plot measures 18 × 14 chains (1 chain = 66 feet) and contains approximately 25 acres of a homogeneous forest type. The circles, spaced at 2-chain intervals, are reference posts to permit rapid orientation within the plot. Lines represent lines of travel used in the census of breeding bird population, and crosses represent the positions of traps used in small mammal census. The other circles, distributed in two sampling clusters of ten trees each, represent trees used in insect population work (cf. Morris 1955a). On the strip (shown only along one line but applying to all lines), forest cover is measured, trees are tagged for annual defoliation and damage records, and small quadrats are established outside the line of travel for the study of ground vegetation.

The present paper is based largely on a combination of data form two of these plots—G4, one of the earliest to be established, and K1, in a focal point of the budworm outbreak. The forest stand on both plots is composed largely of overmature

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balsam fir, *Abies balsamea* (L.) Mill., about 105 years in age and 60-70 feet in height. More detailed descriptions of area and vegetation are reserved for a later paper where plot differences will be treated more specifically.

The technique used for the measurement of spruce budworm population has already been presented in detail (Morris 1955a). By the use of extension ladders and pole pruners, foliage samples are collected from different levels of standing trees and the insect numbers are converted to absolute population, or population per acre, through the measurement of foliage quantity per acre. This work is done throughout the season and includes all stages of the budworm.

The population of small birds is measured each spring by a song census of territorial males, with the general (but not essential) assumption that each territorial male represents a breeding pair of birds. Marked, parallel lines through the plot are traversed on successive mornings and the positions of singing males are plotted. This technique has already been discussed by Kendeigh (1947) and has been further elaborated and standardized in Audubon Field Notes 4: 185-187, 1950. At Green River this census is started in the latter half of June, after all migratory species have arrived and established nesting territories.

Until 1954 the small mammal census was conducted by the well-known mark-and-release method, as modified by Morris (1955b) for use in other parts of eastern Canada. In 1954 the ingenious method proposed by MacLulich (1951) was tested and adopted. By this method a quadrat and a line are trapped simultaneously and the results are substituted in a simple quadratic equation which provides the average range of movement for a specific trapping period. Appropriate adjustments have been made to make the results of the earlier trapping directly comparable to those of the MacLulich method. Trapping is conducted late in the season, when small mammals have reached their annual population peak (*cf.* Morris 1955b), and the results to be presented here include both adults and juveniles. Repeated tests have shown that live-traps and snap-traps are about equally efficient for the common species of the area.

Larger birds and mammals, which cannot be censused on plots of this size, are recorded only by a relative index which consists of the number per mile observed each season during the course of many miles of car, foot, and canoe travel over the Watershed.

The method of analysis and the conclusions as to which predators showed a numerical response to the budworm population also require comment. No doubt it has already occurred to the reader that it is not possible, using population data alone, to distinguish between a true response and a mere fortuity. In fact, since we are working with many species of predators, it would be surprising if one or more species did not increase, quite by chance, at the same time the budworm increased. Fortunately, some bird population records have been taken by other workers during earlier outbreaks of the spruce budworm and during outbreaks in other parts of North America (Maynard 1871, Philipp and Bowdish 1919, Kendeigh 1947, Hensley and Cope 1951). When certain species are found to be unusually abundant during successive budworm outbreaks, and only during these outbreaks, the chance of this being a coincidence becomes increasingly smaller. The procedure in the present analysis has been as follows: (1) Compare the population trend of each species of predator with the population trend of the spruce budworm during the 10-year period of the census. (2) Compare the population levels on the whole series of plots (on some of which the budworm fluctuated at an intermediate level) to learn whether the apparently responsive species reached higher populations where the budworm reached higher populations. (3) Consult the literature to learn whether the same species became unusually abundant in other budworm outbreaks. (4) Consider the apparent response in relation to the known ecology of the predator to see whether there is a sound biological basis for expecting such a response.

Despite this method of analysis, it is altogether possible, or in fact probable, that some of the so-called responses to be discussed here are nothing more than fortuitous events. It is planned to continue the records on both the numerical and functional responses for many years, so if the apparent response of certain species to date is mere coincidence, this should eventually be detected.

The Spruce Budworm

The life history of the spruce budworm has been described in many publications and what is known of its population dynamics to date has recently been summarized by Morris *et al.* (In press). For present purposes we are concerned only with the availability of the budworm as a source of food for birds and mammals.

The budworm overwinters as a very tiny larva in a hibernaculum which is hidden under bud scales or in staminate flower bracts on the tree. Because of its small size and concealment, it does not offer an attractive source of winter food to

either birds or mammals. In any case, the great majority of the bird species of this region are migratory and spend the winter farther south and, with the exception of the red squirrel, the mammals are more terrestrial than arboreal. Development resumes in May and budworm larvae have generally advanced to the fourth instar by the third week of June. Gizzard analyses on large numbers of birds show that the budworm does not become attractive to most species until the fourth instar is reached. In fact, most of the predation occurs in the fifth and sixth instars, which are larger and more freely exposed on the expanding shoots, and in the pupal stage, which also occurs on the foliage. These larger larvae and pupae are available to birds until late July. The migratory birds arrive during May and early June and the nesting territories of most species are usually well defined by mid-June. Budworm larvae and pupae are therefore available to them through the critical period when they are carrying food to the nestlings. In late July and early August the moths are available to birds that capture flying insects, and the egg masses are available on the foliage until late August.

The budworm is available to terrestrial mammals only when populations are extremely high and the resulting shortage of foliage causes many larvae to drop from the trees. This occurs only in severe outbreaks and generally in a limited period in late June and early July.

The population trend for the spruce budworm (Figure 2) applies to the third larval instar, and therefore represents the annual level of the population just prior to the time when the larvae become attractive to birds. In 1945 and 1946 the third-instar population remained very low at about 1,000 larvae per acre. The budworm feeds on new shoots, of which there are about 8 million per acre in mature stands, so a collector (or a bird) would find only one larva for each 8,000 shoots examined. In 1947 population increased to about 5,000 larvae per acre, not an impressive change on the scale of Figure 2 but possibly significant to birds dependent upon a supply of insect larvae to ensure high survival of nestlings. The budworm population reached its peak at 8 million per acre in 1951, an increase of 8,000-fold over its 1945 level. Since then it has been declining, largely as a result of foliage depletion and tree mortality, and particularly because of the great outward dispersal of moths that accompanies these phenomena. Defoliation became severe in 1950, trees started to die in 1954, and tree mortality in this particular stand will be practically complete in another two or three years.

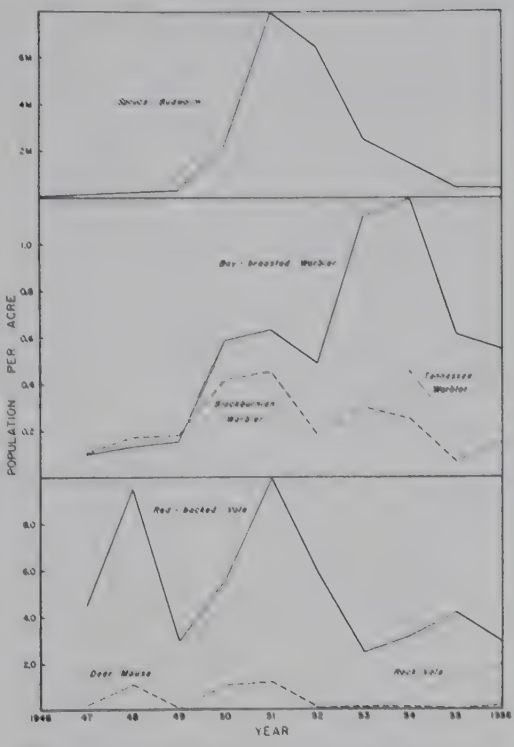

FIG. 2. The comparison of the population trends of the spruce budworm and certain species of birds and mammals. Note that the vertical scales showing population per acre are different for each group and read in millions in the case of the budworm.

THE RESPONSE OF SMALL BIRDS

The apparent numerical response of small birds is shown in Table I and the population trends of the three species that showed the best direct response appear in Figure 2. Table I does not list all the species of small birds that occur in the Green River area, but only those species that were recorded on our plots fairly consistently during the years of the census. Low populations cannot be measured accurately on plots of the size used. If each 20-acre plot has one pair of nesting birds of a certain species, or parts of the territories of more than one pair, it is assumed that the population density is about 5 pairs per 100 acres; but when populations are lower than this they are represented simply by P (Table I) to denote the presence of the species at lower densities than 5 pairs per 100 acres. The use of 100 acres in Table I (and II) is simply a means of avoiding decimal points and is common practice in the tabulation of small bird populations.

Examination of Table I shows that most of the significant responses occurred in the Parulidae,

TABLE I. The common species of small birds, their numerical response during the spruce budworm gradation, and the range in their population densities during the ten-year period 1947-1956. (Response: N = None, D = Direct but weak, DD = Direct and strong, I = Inverse.) (Density: Number of breeding pairs per 100 acres; P = Present but less than 5)

Species	Response	Density
PICIDAE		
Yellow-bellied Sapsucker, *Sphyrapicus varius*	N	P-P
Hairy Woodpecker, *Dendrocopus villosus*	N	P-5
Downy Woodpecker, *Dendrocopus pubescens*	N	P-P
Arctic Three-toed Woodpecker, *Picoides arcticus*	N	P-5
TYRANNIDAE		
Yellow-bellied Flycatcher, *Empidonax flaviventris*	N	P-10
Least Flycatcher, *Empidonax minimus*	N	P-10
Olive-sided Flycatcher, *Nuttalornis borealis*	N	P-P
CORVIDAE		
Canada Jay, *Perisoreus canadensis*	N	P-5
Blue Jay, *Cyanocitta cristata*	N	P-P
PARIDAE		
Black-capped Chickadee, *Parus atricapillus*	N	P-10
Hudsonian Chickadee, *Parus hudsonicus*	N	P-5
SITTIDAE		
White-breasted Nuthatch, *Sitta carolinensis*	N	P-5
Red-breasted Nuthatch, *Sitta canadensis*	N	P-15
CERTHIIDAE		
Brown Creeper, *Certhia familiaris*	N	P-5
TROGLODYTIDAE		
Winter Wren, *Troglodytes troglodytes*	I	P-20
TURDIDAE		
Robin, *Turdus migratorius*	N	P-P
Olive-backed Thrush, *Hylocichla ustulata*	D	P-30
SYLVIIDAE		
Golden-crowned Kinglet, *Regulus satrapa*	N	P-15
Ruby-crowned Kinglet, *Regulus calendula*	N	P-P
VIREONIDAE		
Blue-headed Vireo, *Vireo solitarius*	N	P-15
PARULIDAE		
Tennessee Warbler, *Vermivora peregrina*	DD	0-45
Parula Warbler, *Parula americana*	N	P-10
Magnolia Warbler, *Dendroica magnolia*	I	P-35
Cape May Warbler, *Dendroica tigrina*	N	P-P
Myrtle Warbler, *Dendroica coronata*	I	P-20
Black-throated Green Warbler, *Dendroica virens*	I	P-25
Blackburnian Warbler, *Dendroica fusca*	DD	5-45
Bay-breasted Warbler, *Denaroica castanea*	DD	10-120
Black-poll Warbler, *Dendroica striata*	N	P-10
Ovenbird, *Seiurus aurocapillus*	D	P-10
Redstart, *Setophaga ruticilla*	N	P-5
FRINGILLIDAE		
Evening Grosbeak, *Hesperiphona vespertina*	D	0-P
Purple Finch, *Carpodacus purpureus*	N	P-5
Pine Grosbeak, *Pinicola enucleator*	N	P-5
Slate-colored Junco, *Junco hyemalis*	N	P-15
White-throated Sparrow, *Zonotrichia albicollis*	N	P-15
All species		200-355

or wood warblers. This was not surprising. During outbreaks many species of birds alter their normal feeding habits to take advantage of the copious food supply and we have frequently observed ground-feeders, cross-bills, and even woodpeckers, picking budworm larvae from the foliage of balsam trees. However, a numerical response is more to be expected in those species that normally search coniferous foliage and depend largely upon defoliating larvae for themselves and their nestlings. The warblers meet these specifications better than any other family. Moreover, they are all migratory. Resident birds like the woodpeckers, jays, and chickadees, are more likely to be limited in numbers by the availability of food during the cold winter months than during the brief spring nesting period. It is well known that adults of many migratory birds, including the warblers, usually return to the same nesting territories and that the nestlings of the previous year return to the same general area to search for vacant territories. Assuming that the availability of food for nestlings is a factor limiting the growth of warbler population up to the point where all available territories are occupied (*cf.* Lack 1954), an appreciable increase in budworm population one spring should be followed within a year or two by a recognizable increase in warbler population.

The response of the bay-breasted warbler (Fig. 2) was almost immediate and its 12-fold population increase (10 pairs to 120 pairs per 100 acres) was greater than that for any other species. As would be expected, it reached its peak somewhat later than the budworm peak. The response of the blackburnian warbler was equally early but not nearly so great. These two warblers occupy very similar, or perhaps identical, niches in the upper levels of coniferous trees and inter-species competition probably becomes intense as the territorial saturation point is approached. The trends in Figure 2 suggest that the bay-breasted warbler is the more aggressive competitor. Both warblers, in common with many other migratory species, showed unexpected drops in 1952. High warbler mortality due to unseasonable spring water is common and Graham and Orr (1940) refer to two decimations, one in 1907 and another in 1910. They occurred just prior to a budworm outbreak in Minnesota and Graham and Orr suggest that they were at least partly responsible for the release of the budworm population. The Tennessee warbler, which was not even recorded on these plots until 1953, responded very late in the budworm outbreak and it is questionable, therefore, whether it would respond to the shorter gradations that may occur between outbreaks.

Kendeigh (1947) made a breeding bird census in 1945 during the Lake Nipigon outbreak in Ontario and compared his results to earlier census data for coniferous forests in North America. He concluded that the bay-breasted warbler (92 pairs per 100 acres or 10 times what he believed normal), Tennessee warbler (59 pairs), and Cape May warbler (28 pairs) had become unusually abundant during the spruce budworm outbreak. Hensley and Cope (1951) listed populations for

northern Maine in 1949 and 1950 during a gradation of the spruce budworm which preceded the New Brunswick gradation but which did not reach severe outbreak proportions. The same three warblers were predominant along with the blackburnian, which increased its numbers between 1949 and 1950. An earlier outbreak of the spruce budworm in New Brunswick started in 1912 and Philipp and Bowdish (1919) reported increases in the bay-breasted and Cape May warblers. Kendeigh summarizes records showing that these two species and the Tennessee warbler increased during the outbreak of the same period in the eastern states. In fact, there is rather good evidence that the same species increased during an even earlier outbreak (1870-80) and afterwards declined (Maynard 1871; and other work reviewed by Kendeigh).

There is little doubt, therefore, that spruce budworm outbreaks are accompanied by "outbreaks" of certain warblers, particularly the bay-breasted warbler. For reasons not understood, the Cape May warbler has not responded to the present outbreak at Green River, although it has apparently responded to earlier outbreaks in other parts of New Brunswick. On the other hand, the blackburnian warbler has responded to the present outbreak but apparently not to earlier ones.

A direct but moderate response was shown by the olive-backed thrush (Table I) and this species doubled its population in northern Maine between 1949 and 1950 (Hensley and Cope 1951). Considering the absence of data for earlier outbreaks, however, as well as the fact that members of this family take much of their food from the ground, this apparent response may be fortuitous. During recent years the evening grosbeak has greatly extended its summer breeding range and increased in numbers in areas under budworm attack (cf. Shaub 1956). Before the present outbreak it was rarely seen in northern New Brunswick in the summer, but large flocks are now a common sight throughout the infested area. Whether this represents a response to budworm numbers or to other factors is difficult to judge at this time.

Among the warblers the magnolia, myrtle, and black-throated green showed inverse responses. Kendeigh reported that the same three species, and the parula warbler, were much scarcer than normal in the Nipigon outbreak. In both cases the magnolia was the species that showed the greatest decline, the density at Green River decreasing from 35 pairs per 100 acres before the outbreak to less than 5 pairs towards the end. Kendeigh believed that this type of response was the result of inter-specific competition with more aggressive species like the bay-breasted warbler. The winter wren also declined (Table I) but as this is a species which occupies a lower stratum of vegetation, this apparent response was probably coincidental.

The response of all species considered together was direct, the population increasing from 200 to 355 pairs per 100 acres. The total population on Kendeigh's plots was 319 pairs per 100 acres and he believed that this was an extraordinarily high breeding population for a coniferous forest, when compared with records during low budworm populations in North America and with the populations of less than 100 pairs per 100 acres reported for coniferous forests in Finland.

The Response of Small Mammals

It has already been indicated that the spruce budworm is available to small terrestrial mammals only under special circumstances, and even then only for a small portion of their breeding season. Further, with the exception of the jumping mouse, the small mammals of this area do not hibernate so it would be expected that the availability of winter food or the effect of winter predation would be more likely to limit their numbers than a brief supply of perishable summer food.

The short-tailed shrew (Table II) was recorded at very low populations until 1955, when it started to increase rapidly and reached a population of 60 animals per 100 acres in 1956. This apparent response seems to be far too late to be directly related to the spruce budworm population. The rock vole is a rather rare rodent that was recorded in New Brunswick on only two occasions prior to 1954. In that year a number of specimens were taken on those plots that lay within the severe infestation area and by 1956 it had reached

Table II. The common species of small mammals, their numerical responses during the spruce budworm gradation, and the range in their population densities during the ten-year period 1947-1956. (Response: N = None, D = Direct but weak, I = Inverse.) (Density: Number of animals per 100 acres; P = Present but less than 10)

Species	Response	Density
SORICIDAE		
Cinereous Shrew, *Sorex cinereus*	N	P-70
Pigmy Shrew, *Microsorex hoyi*	N	P-P
Short-tailed Shrew, *Blarina brevicauda*	D?	P-60
CRICETIDAE		
Deer Mouse, *Peromyscus maniculatus*	I?	P-120
Lemming Vole, *Synaptomys cooperi*	N	P-30
Lemming Vole, *Synaptomys borealis*	N	P-10
Red-backed Vole, *Clethrionomys gapperi*	I?	250-960
Meadow Vole, *Microtis pennsylvanicus*	N	P-10
Rock Vole, *Microtis chrotorrhinus*	D?	P-180
ZAPODIDAE		
Woodland Jumping Mouse, *Napaeozapus insignis*	N	P-10
All species		270-1130

a population of 180 on the same plots (Fig. 2). It is difficult to attribute this unique increase of a rare species to the spruce budworm population, at least in any direct way. Perhaps it is more logical to speculate that the decrease in the population of the red-backed vole has in some way relieved the rock vole from interspecific competition.

The red-backed vole is by far the most abundant small mammal in the area and usually comprises some 90 percent of the whole population. It has population peaks at intervals of three or four years, when it reaches a density of about 1,000 animals per 100 acres. In the 1955 peak, however, it did not reach half this density (Fig. 2). The deer mouse, which has similar but much lower peaks, did not show any peak at all in 1955. This could scarcely be a direct result of the budworm outbreak but it may possibly be an indirect result. Severe defoliation and tree mortality have so reduced the supply of balsam seed that the rodents may have been deprived of their main source of winter food. It is interesting to note that the rodent peaks in 1948 and 1951 coincided with peak years of balsam seed availability in this area but it is too early to assume that this represents cause and effect (cf. Lauckhart 1957). Again, the destruction of the overstory has undoubtedly altered the physical habitat of small mammals. Whether these factors are involved in the apparent direct or inverse responses of the various species of small mammals can only be ascertained by continuing the population work for additional years in the dying forest.

The Response of Larger Birds and Mammals

Of the various larger species covered by our annual census of relative abundance, only the ruffed grouse, *Bonasa umbellus,* and the red squirrel, *Tamiasciurus hudsonicus,* are likely to be of any importance as budworm predators. Both species, however, must search for food during the winter months so it is not surprising that their populations did not show any direct response to budworm populations. The ruffed grouse had high populations between 1946-48, decreased to a low in 1952, and has since been increasing. The red squirrel increased to a very high peak in 1951, when it became so numerous that small mammal trapping was very difficult because squirrels overturned the traps. This unusually high population crashed in 1952 and has not yet shown much evidence of recovery from the crash. It is possible that this lack of recovery is associated with the budworm-induced shortage of coniferous seed (*cf.* Vartio 1946).

Similarly, as a result of stand mortality rather than an immediate result of budworm numbers, many larger species may reveal a belated response to the outbreak. The white-tailed deer, for instance, might be expected to find better food and cover in the dense reproduction and shrub growth that becomes established after the destruction of the coniferous overstory. An event of such ecological magnitude could hardly fail to have its ramifications throughout the populations of all forest animals. There is no point in speculating upon these ramifications, however, when the continuation of the work may reveal their results in a quantitative way.

Discussion

The effect of birds and mammals on the budworm population during the outbreak years has been negligible. The budworm increased 8,000-fold while the most responsive predator—the bay-breasted warbler—increased only 12-fold. On the basis of rather general data, Kendeigh (1947) estimated that one pair of breeding birds plus their nestlings could consume 16,000 budworm larvae and pupae during the period of availability. George and Mitchell (1948) estimated 14,000 on the basis of mean food capacity. Both estimates were based on the assumption that birds would feed exclusively on the budworm during outbreaks. Actually, subsequent gizzard analyses by Mitchell (1952) showed that even when the budworm was quite numerous in northern Maine in 1950, it comprised only 40 percent of the diet of insectivorous birds. Forty percent of a potential 15,000 gives 6,000 budworms per acre as a closer estimate of actual consumption per breeding pair, or very roughly 20,000 per acre for all the bird species that feed largely on foliage insects. Dowden *et al.* (1953) estimated actual consumption at about 36,000 per acre in northern Maine. At the peak Green River budworm population of 8 million larvae per acre, therefore, the predation caused by birds would be less than one percent.

However, when the budworm population is fluctuating about its endemic level of 1,000 or less per acre birds could be extremely important, even if the budworm comprised far less than 40 percent of their diet. Mortality of larvae and pupae from other sources would rarely be less than 50 percent (Morris *et al.,* in press), so a bird population with a total feeding capacity of 30,000 larvae and pupae per acre (2 pairs of birds per acre before the outbreak with a total food capacity of 15,000 budworms per pair) would have to include only about 2 percent budworm material in the diet to account for the remaining 500 insects. Another point of importance is that the attack by birds occurs in a period when the mortality caused by parasites and other factors is also high. Because

of this high level of contemporaneous mortality, comparatively small variations in predation could have a very drastic influence on population trend (Morris 1957).

As explained earlier, however, the real decision as to whether birds can act as regulators during the long endemic period must be based upon their numerical and functional responses. The present study shows that certain species of birds, notably the bay-breasted warbler, exhibited the proper type of numerical response to a budworm population that was increasing rapidly toward the epidemic level. Also, this response seemed to occur rather early in the gradation, although definite conclusions on timing are not possible because the situation was complicated by high populations of the black-headed budworm, *Acleris variana* (Fern.) in the same area in 1947 and 1948. It is interesting to speculate that the surplus of food provided by *A. variana* in those two years may have relieved predation pressure on the spruce budworm and thus contributed to the development of the outbreak. However, the analysis of the functional response, which will follow the interesting leads opened by Tinbergen (1949) and Betts (1955) is essential before problems of this type can be resolved.

As a contribution in population dynamics the present study, like others conducted during the course of a severe outbreak, has been disappointing. We have learned mainly that the upper limit of budworm numbers is determined by foliage depletion; a fact readily deducible in advance from the extensive pattern of forest destruction in earlier outbreaks. We have learned that certain biotic factors such as birds and parasites responded directly but ineffectually to a rapid and sustained increase in budworm population. Will they show a more effective response to the lesser gradations that may occur between outbreak periods? The interesting part of the study must await the resumption of endemic population levels, when our primary concern will be to learn to what extent the budworm is under density-responsive regulation during the periods between outbreaks and to what extent its numbers simply vary under the influence of chance, weather, and changes in the age and structure of the forest.

Summary

The study of the effects of predators on a given species of prey is concerned largely with two responses—the numerical response of predator populations to changes in the population density of the prey, and the functional response or change in the food habits of the predators associated with the increasing or decreasing availability of a certain food. Both types of predator response are being measured during a long-term study on the population dynamics of the spruce budworm on the Green River Watershed in northern New Brunswick, Canada. The present paper is restricted to a brief review of the numerical response of birds and mammals during the 10-year period 1947-1956. In some of the forest stands under study the budworm reached outbreak proportions and killed trees during this period, while in others the gradation was much less severe. A direct numerical response was shown by some birds and particularly by three wood warblers—the bay-breasted, blackburnian, and Tennessee. Some other warblers—the magnolia, myrtle, and black-throated green—showed an inverse response, presumably due to interspecific competition with the species that showed a direct response. During the same period the population of rodents and insectivores showed no response but fluctuated independently of budworm density; however, the decreased heights of the peaks in the cycles of the red-backed vole and the deer mouse may have been associated with a shortage of tree seed resulting from budworm damage. Predators were of little control value during the outbreak. However, the direct numerical response of certain birds at least gives them one of the properties essential in regulation, and the continuation of the work should reveal whether such regulation occurs when the budworm is fluctuating at its low, endemic level.

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NICHE RELATIONS OF THREE SPECIES OF LYCOSID SPIDERS[1]

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INTRODUCTION

Although spiders are conspicuous in terrestrial communities and undoubtedly play an important part as carnivores in the energy budget, they have been neglected from the ecological standpoint until rather recently. Barnes (1953) briefly reviewed previous papers concerned with spider ecology and presented the results of his own study of the structure of spider populations of the several nonforest maritime plant communities of the North Carolina coast. This same type of qualitative and quantitative analysis was continued by the team of Barnes and Barnes (1954, 1955) for the spider populations of maritime drift lines and broomsedge communities. A slightly earlier paper by Norgaard (1951) shows quite clearly how the differences in the microclimate within a sphagnum bog community may effectively separate two related species with different habitat preferences and environmental tolerances. Recently, Hackman (1957) has published extensive data on the population dynamics of the wolf spider, *Trochosa,* in Finland using a marking technic similar to that employed in this study.

The members of the family Lycosidae, the wolf spiders, are active hunters which do not depend on a web to snare their prey. A good description of the family may be found in Gertsch (1949). The species *Lycosa carolinensis* Walckenaer, *L. timuqua* Wallace, and *L. rabida* Walckenaer were selected for this study because of their abundance in old-field ecosystems, their relatively large size which permitted the use of a simple marking technique, and the fact that they are nocturnal and their eyes strongly reflect the light from a headlamp. This characteristic greatly simplifies the location of individuals which might otherwise be well camouflaged. The present investigation was designed to determine the niche relations of these species.

Lycosa carolinensis, a common spider over the greater part of the United States, digs burrows in the soil, to which it retreats in the daytime or when alarmed; these have been described and illustrated by Gertsch (1949) as well as others. *Lycosa timuqua,* a Southeastern coastal plain species, also digs an inclined burrow, the entrance to which is covered by a hinged trap door composed of loose duff and sand held together underneath with silk. This is similar to the burrows of the closely related species, *L. lenta* and *L. ammophila,* as described briefly by Wallace (1942). *Lycosa rabida,* also widely distributed in the United States, does not burrow but may spin an irregular sheet-like web on which to rest, as described by Montgomery (1903) and Truman (1942). An

[1] This investigation is one of a series of ecological studies on the Savannah River Plant area supported by a grant from the U. S. Atomic Energy Commission (Contract AT (07-2)-10).

active climber in the forbs and grasses, it is reported by Barnes (1953) to stay usually above the ground. The study by Bilsing (1920) in which 25 species of insects from eight different orders were eaten by one captive *L. carolinensis* indicates the nonspecificity of the lycosid diet.

Field work for this investigation was done in Aiken County, South Carolina, on the Savannah River Plant (SRP) Area which lies on the Upper Coastal Plain at a point characterized by rolling topography and sandy soils. Because of the unique ecological opportunities provided, the old-field ecosystems of the area are being intensively studied by a student-faculty research group of the University of Georgia. Lycosid spiders are one of the important ecological components which are under investigation.

The author is especially grateful to Dr. Eugene P. Odum for his encouragement, his many worthwhile suggestions, and his critical reading of the manuscript. Dr. H. K. Wallace was very kind in identifying the lycosids, in offering unpublished notes and suggestions concerned with this study, and in criticizing the manuscript. Mr. Karle E. Herde of the Savannah River Operations Office of the A. E. C. was very helpful in making arrangements for carrying out field work.

Methods

During June and July, 1952, species composition and density of lycosids were determined on ten areas representing the principal stages of old-field succession and several of the important forest types. In each area, one large quadrat of 100 square meters was laid out and all lycosids that could be found in a single night of favorable weather were collected and preserved for identification. Random collections were also made in the vicinity of these quadrats and in other areas from April until July, 1952.

During midsummer of 1953 four quadrats of one-tenth hectare (one-quarter acre) were laid out and each was subdivided into a grid of one hundred squares by means of strings. Numbered tabs on these strings made it possible for the investigator to remain constantly oriented. One of these quadrats was located in each of the following habitats: (1) Burned-over old-field, 90 percent open sand with scattered clumps of short grass and a few small shrubs; (2) Longleaf pine-turkey oak scrub (*Pinus palustris, Quercus laevis*), mostly open sand with patches of pine-needle litter and a few small shrubs; (3) Broomsedge field, 75 percent coverage of three foot *Andropogon virginicus;* (4) Slash pine woods (*Pinus Elliotti*), trees planted about 20 years previously and the ground completely covered with needles with a few sprigs of *Andropogon* sp. still present. During late spring of 1954 two more quadrats were prepared as before, one in each of the following habitats: (5) Slash pine woods, same grove as No. 4 about 100 meters away and, except for the absence of *Andropogon,* apparently an identical habitat; (6) Abandoned field, mixed growth of forbs, mostly *Heterotheca subaxillaris.* The quadrats were visited nightly when possible over a period of nineteen days in 1953 and thirty-six days in 1954.

The handling of the individual spiders was quite simple. They were urged to climb into a shell vial placed in front of them by gently prodding from behind. While the spider rested quietly in the vial it was possible to determine if it was male, female, or immature. Unfortunately the various immature instars could not be aged. A gentle shake of the vial near the ground would then dislodge the spider and it would usually remain quietly on the ground while the proper segments of its legs were marked with dots of white enamel according to a predetermined numbering system. The state of maturity, sex, and location on the grid were recorded, along with general notes such as feeding, copulating, and carrying egg sac or young. Occasionally the spider would be at the entrance or would retreat to its burrow. Each time a marked spider was seen on subsequent nights its position on the grid was recorded and this constituted another capture or recapture although the spider was not actually handled again.

The 1954 study of quadrats 5 and 6 included measurement of the barometric pressure, temperature, and relative humidity, and estimation of wind, cloud-cover, and moonlight. Temperatures and relative humidities were measured with a hand-aspirated psychrometer at the surface of the ground at the beginning and end of each visit to each quadrat.

Results

General Behavior

Both *Lycosa carolinensis* and *L. timuqua* are ordinarily found on the ground but, although they usually run away over the surface when disturbed and the burrow isn't handy, they occasionally climb, especially the smaller immatures. These two spiders also frequently use mouse burrows (*Peromyscus p. polionotus*) as retreats when disturbed at night and may occasionally be found under stones or boards in the daytime. The climbing of *Lycosa rabida* has already been mentioned and this spider, when disturbed, is capable of remarkably fast dashes through the vegetation. In open woods it is frequently found on the lower

trunk or branches of the trees. The capture and marking procedure was more difficult with *L. rabida* because of the excitability of this species. These spiders would usually quickly retreat before the investigator, leaping or scrambling from their positions high on the grass into the thicker grass near the ground, or they would parry the lips of the vial with their first pair of legs and hesitate to enter. Hesitancy to enter a tube may be due to the fact that since they do not burrow they do not have the proper type thigmotaxis which causes the other two species to enter. Often the spider would run when the enamel was applied to the first of the required segments, necessitating a relentless follow-up until all of the proper segments had been marked. Sometimes the spider would attack the enamel brush itself and get a coat of enamel on its fore-legs, pedipalps and chelicerae, probably resulting in premature death.

Field notes on the foods actually in process of ingestion when the spiders were observed are here listed by common name since the spiders were not disturbed by taking away the food for better identification. *Lycosa timuqua:* three grasshoppers, three moths, three beetles, and one each horsefly, wasp, cricket, caterpillar, and another spider. *Lycosa carolinenis:* two roaches and one each moth, katydid, and *L. timuqua*. *Lycosa rabida:* three caterpillars and one each grasshopper, beetle, moth, roach, and another *L. rabida*. In a series of eighteen "forced" interactions in which individuals of *L. timuqua* or *L. carolinensis* were picked up in the field and placed near other individuals of the same or opposite species it was found that both species are cannibalistic, that each species will eat the other, and that generally the larger individual is successful during any one conflict. Individuals of approximately the same size usually ran from each other or, when one did attack, they quickly separated with no apparent harm to either. It may be safely assumed that all three species of *Lycosa* are subject to both inter- and intra-specific predation.

Habitat selection

Table I shows the densities of the ten most abundant species of lycosids collected in one night from 100 square meter quadrats located in several types of old-field and forest communities of the SRP Area. This table might be considered as a semi-successional chart since the quadrats sampled represent, from left to right, increasing age and/or humidity of the habitats, especially quadrats one through five. *Lycosa carolinensis* and *L. timqua* are both found in abundance beginning with the first year of abandonment of fields and persist through many succeeding stages. Although

TABLE I. Number of Lycosid Spiders found within a quadrat of 100 square meters in a series of habitats* on the SRP in June-July, 1952

Species	Old Fields					Open Scrub Forests		Upland Forests		Flood Plain Forest
	1	2	3	4	5	6	7	8	9	10
Pardosa georgiae Chamberlin & Ivie	15	13								
Schizocosa avida Walck.		P			2	2				
Lycosa carolinensis Walck.	8	P	2	5		4	1			
Lycosa timuqua Wallace	1	11	15	54	6	28	1	1	15	1
Lycosa rabida Walck.	P	P	2	1	27	1	13	4	1	
Lycosa hentzi Banks	P	P			P	7	1		P	
Schizocosa duplex Chamberlin						2	3	37		
Lycosa riparia Hentz									P	10
Schizocosa crassipes Walck.									26	12
Schizocosa ocreata Hentz										3

*1. First year field (cotton in 1951); 60% coverage of forbs, mostly *Leptilon*.
2. First year field (corn in 1951); 30% coverage of forbs, mostly *Leptilon*.
3. Second year field (corn in 1950); 95% coverage of *Haplopappus*, *Cassia*, and *Leptilon*.
4. Third or fourth year field; 12% coverage of forbs, mostly *Haplopappus*.
5. Broomsedge field; five or more years old, 90% *Andropogon*.
6. Longleaf pine-turkey oak scrub (*Pinus palustris*, *Quercus laevis*); sparse understory.
7. Pine scrub; 10% canopy of *Pinus Elliotti*, 50% understory coverage of *Diospyros*, *Crataegus*, *Rhus*, *Cornus*, *Liquidambar*, and *Quercus* spp.
8. Planted pine woods; *Pinus Elliotti*, no understory, complete mat of needles
9. Deciduous hillside; *Quercus alba* dominant with some *Carya* and *Liquidambar*, understory of *Cornus*, *Celtis georgiana*, and *Nyssa sylvatica*.
10. Flood-plain forest; 95% canopy of *Liquidambar* and *Quercus nigra* with some *Acer rubrum*, understory mostly small *A. rubrum*, *Ilex opaca*, and *Liriodendron*.

Note; The letter "P" indicates that although the species was not found within the quadrat it was present in random collections taken near-by.

L. timuqua was found in every type of habitat studied the individual taken in the flood plain forest was an immature and probably wandered into the area rather than being a normal member of the community. Immatures of *L. rabida* were found in the first year fields but this species does not become important in the successional picture until the fields reach the broomsedge stage, which usually begins about five to six years after cultivation ceases, and it persists in the dry woods only as long as the understory is adequate. Because of the difficulty in distinguishing the females and immatures of the two species, the numbers of individuals of *Schizocosa crassipes* and *S. ocreata* listed may be somewhat in error. The table then, indicates the habitats utilized by the three species under study as well as the presence of several other species of lycosid spiders which may at various times act as their competitors, prey, or perhaps even predators.

Population density

Table II depicts the densities of the three spiders in the six quadrats intensively studied using

TABLE II. The number and distribution of adult and sub-adult lycosid spiders on a one-tenth hectare quadrat. The spider distribution is compared to the expected Poisson distribution

Species	Quadrat	No. spiders marked per quadrat	Chi Square from Poisson distribution	Degrees of Freedom
L. timuqua	1	31	8.90*	2
	2	19	9.58*	3
	3	15	5.51	2
	4	16	0.09	2
	5	45	0.78	3
	6	134	1.14	4
L. carolinensis	1	9	.....	
	2	16	0.09	2
	3	3	.....	
	4	3	.....	
	5	23	4.04	2
	6	15	0.05	2
L. rabida	1	0	.....	
	2	2	.....	
	3	70	17.30*	4
	4	16	0.09	2
	5	0	.....	
	6	0	.....	

*Significant at 5-percent level.

the mark-and-recapture technique. *Lycosa timuqua* and *L. carolinensis* were found in all quadrats with the former more abundant. Only in the longleaf pine-turkey oak scrub quadrat (2) are the densities approximately equal. *Lycosa rabida* dominated the broomsedge quadrat (3) and was equally abundant with *L. timuqua* in the planted pine woods (4) where a little broomsedge was still present. The fact that *L. rabida* was not found in the similar pine woods (5) which had no broomsedge the following year substantiates the view that it requires a more dense vegetation than mere tree trunks upon which to climb. The values in Tables I and II are reasonably comparable in terms of relative abundance in each type of habitat.

Some explanation should be given concerning the estimate of spider density in Table II. Since only the larger individuals, *i.e.,* adults and subadults, were marked, the estimated number of spiders of all three species is obviously too low. Many small immatures were seen but ignored because of the difficulty involved in marking them successfully. The estimate would also tend to be low if, as possibly happened, a few individuals within the quadrat were never seen. On the other hand the investigator strongly suspected several times that an unmarked spider appearing after the study had been underway for several weeks was simply a previously marked individual which had molted. This shedding of the mark, exposing the spider to subsequent capture and remarking with a new number, would tend to raise the estimate of the population density. The previously mentioned difficulty encountered in marking *L. rabida* certainly has caused an underestimation, perhaps of as much as 50 percent of its real density.

Cole (1946) demonstrated that of all the small animals which he sampled in a woodland, only the spiders were randomly distributed. The last column of Table II shows how the lycosids in the present study were distributed within the study quadrats. The location at which each spider was first captured, hence prior to having been disturbed by the investigator, was plotted on a grid of 100 squares which represented the original one-tenth hectare quadrat. Then the number of squares with 0, 1, 2, *etc.,* spiders was compared with the expected random (Poisson) distribution. The values of Chi-square in Table II strongly indicate random distribution for all these lycosids except in the case of *L. timuqua* in quadrats 1 and 2, and *L. rabida* in number 3. It is suggested that the apparently non-random distribution of *L. timuqua* in those cases is due to non-uniformities within the habitat which were undetectable to the investigator. *Lycosa carolinensis* proved to be randomly distributed in number 2 indicating that this species did not respond to the same microhabitat differences as did *L. timuqua.* Although an attempt was made to establish all study quadrats in very uniform habitats, it became noticeable after working in number 3 for several nights that the broomsedge was actually taller and more dense on one half of the quadrat. The plotting of the field data showed clearly that *L. rabida* was actually more abundant in the denser half, hence was not randomly distributed. Note that *L. timuqua* was not so affected by this difference in broomsedge density.

Home range

The size of the area over which an animal ranges during its normal movements has been of particular interest to persons studying birds and mammals and to a lesser extent to students of invertebrates and cold-blooded vertebrates. These studies have given rise to the concepts of home range (when the area is not defended) and territory (when it is defended). The major problem in studies of home range is the accurate estimation of the area actually utilized; therefore legitimate comparisons of home range size between various species or even between individuals of the same species when studied by different persons are quite difficult.

The first method attempted with the lycosid data consisted of plotting the points at which each individual spider was located on nights subsequent to its initial capture and connecting the

outermost recapture loci to form a polygon. The area of this polygon is the estimate of home range shown in Table III. Only those individuals captured four or more times have been included in

TABLE III. Home range size in three species of *Lycosa* obtained from the area of the polygon constructed around the outermost recapture loci of each spider captured four or more times

Species	Sex	Number of Spiders	Ave. Number of Captures	Average Home Range (Feet^2)
L. timuqua	Immatures	27	5.5	33
	Males	2	5.5	449
	Females	8	5.8	103
L. carolinensis	Immatures	3	5.0	6
L. rabiaa	Immatures	2	4.5	130

the table. Except for the males of *L. timuqua,* who very likely were undergoing pre-courtship wanderings, all home ranges are relatively small with that of *L. rabida* being largest. It is recognized that as few as four recaptures do not adequately define the area which a spider may actually utilize, hence only a very rough, probably minimum, approximation results. Odum and Kuenzler (1955) introduced a refinement of this method, when used to measure territory size in birds, by constructing an area-observation curve for each pair of birds studied and utilizing the decreasing slope as more and more observations were made to determine the point of diminishing returns, *i.e.,* when continued observations failed to increase substantially the apparent territory size. Unfortunately, an insufficient number of recaptures was made with the lycosids to use their method.

The second method, first proposed by Dice and Clark (1952) and illustrated with data from a deermouse population, consisted in this study of measuring the distance of each recapture locus from the center of activity of every spider which was recaptured two or more times, and constructing for each species a frequency histogram of the square roots of these "activity radii" as shown in Figure 1. When the location of the spider's burrow was known (in the case of *L. timuqua* and *L. carolinensis*) this was considered to be the center of activity, otherwise the approximate geometrical center of the recapture points was used. Computation of β_1 (skewness) and β_2 (kurtosis) followed the procedure of Croxton (1953). In a normal curve β_1 is equal to zero and β_2 is equal to three. The most interesting comparison in Figure 1 is between the nonburrowing *L. rabida* and the two burrowers. The histograms of the burrowers are markedly leptokurtotic, indicating that the major part of their above-ground time is

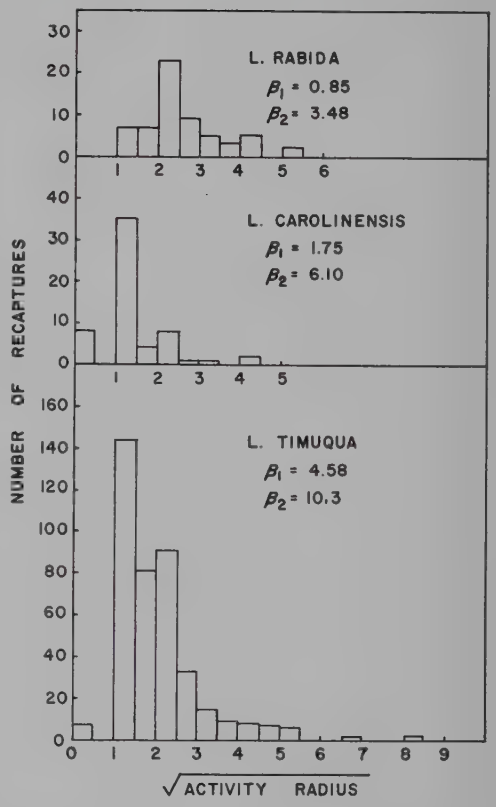

FIG. 1. Frequency histograms of square roots of activity radii (from burrow or center of activity) in *L. timuqua, L. carolinensis,* and *L. rabida.* In a normal curve β_1 is equal to zero and β_2 is equal to three.

spent at a particular distance from the center of activity (presumably the burrow itself) while the positive skewness indicates that this distance is usually less than about 9 feet for *L. timuqua* (three feet squared) and about 2.25 feet for *L. carolinensis* (1.5 feet squared). The histogram for *L. rabida,* although slightly skewed positively, is approximately normal which indicates that this species wanders more-or-less at random over its home range. *Lycosa rabida* also has a larger home range than the other two lycosids.

Effects of weather on activity

Since *Lycosa rabida* was not present in either of the quadrats when notes on weather were made in 1954, the effects of weather apply only to the other two species. No clear cut correlation was seen between such factors as barometric pressure, wind velocity, cloud cover, or amount of moonlight and the relative abundance of lycosids during the study periods. Figure 2 depicts the rela-

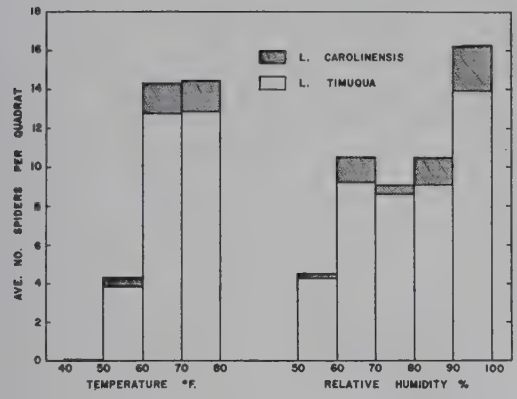

FIG. 2. Effect of temperature and relative humidity on the activity of *L. timqua* and *L. carolinensis* as indicated by the average number of spiders per quadrat outside their burrows. The number of nights during which observations were made in each range of temperatures was: 40°-50°, 1; 50°-60°, 11; 60°-70°, 16; and 70°-80°, 7. The number of nights in each range of RH was: 50-60%, 4; 60-70%, 8; 70-80%, 8; 80-90%, 7; and 90-100%, 8.

tive abundance of *L. tumuqua* and *L. carolinensis* outside their burrows at various ranges of temperature and humidity. Too few observations were made at temperatures below 50°F to draw definite conclusions but there appears to be a temperature threshold near 50°F below which these spiders remain in their burrows and above which an increase in temperature brings an increase in activity, leveling off near 60°F. No such threshold is seen in the relative humidity graph, but there is apparently more activity at higher relative humidities. Since during the night the temperature almost always goes down while the relative humidity is rising, these two effects might seem to cancel each other. Actually these lycosids were much less abundant after about 2:00 A.M. than earlier suggesting that the drop in temperature had the greater effect. Both species seem to react equally to the same factors, *i.e.*, both have their peaks of activity under the same weather conditions.

Discussion

Where *Lycosa rabida* occurs in the same habitats with either *L. timuqua* or *L. carolinensis* the primary factor that separates it ecologically seems to be vertical stratification. *Lycosa rabida* tends to remain above the surface of the ground in the forbs, grasses, or on small trees and shrubs while the other two remain on or below the surface.

The factors that separate *L. timuqua* from *L. carolinensis* are not so apparent. Both tend to forage for the same types of food over the surface of the ground in the same habitats and dig their burrows in the same substrate. Both are active the same time of night and in the same types of weather. On the basis of this study the differences in niches of these burrowers are primarily conjectural. In most habitats *L. timuqua* was the dominant species. Although cannibalism is present and inter-specific predation probably occurs in both directions, with victory going to the larger individual, the small home ranges of the burrowers may reduce interactions to a minimum. Other predators and parasites may exert differential pressures on the two species. The door of the *L. timuqua* burrow which makes the entrance practically undetectable may be especially important as a protective device. A more intensive study of these two species where they occur together should bring to light the real differences in their niches, if any.

Summary

Three species of large, nocturnal wolf spiders, *Lycosa carolinensis, L. timuqua,* and *L. rabida,* were studied in various sandy coastal plain habitats of Aiken County, South Carolina. The position of these species in relation to seven other lycosids in the upland Sere was worked out (Table I). A simple mark-and-recapture method was utilized on 6 one-tenth hectare quadrats to determine spatial relations. In general, *L. timuqua* proved to be the most abundant of the three in all types of habitat studied except where there was an abundance of broomsedge in fields or a reasonably dense understory in scrub woods, in which case *L. rabida* was more numerous. Home range was represented in two ways. The first, as an irregular polygon with corners formed by recapture loci, gave a crude estimate because of the small number of recaptures but indicated a small home range for each species. The second representation, a frequency histogram of the square roots of activity radii, confirmed the small home range and also showed that the burrowers, *L. carolinensis* and *L. timuqua* center their activity around the burrow while *L. rabida,* a non-burrower, wanders more nearly at random over its home range. The distribution of the spiders within any one uniform habitat was usually random. The activities of *L. carolinensis* and *L. timuqua* proved to be positively correlated with temperature and relative humidity. The primary ecological factor separating *L. rabida* from the other two seems to be vertical stratification since *L. rabida* is more frequently found above the ground surface. The exact differences in the niches of *L. timuqua* and *L. carolinensis* are not apparent from this study.

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EFFECT OF AGGREGATION OF LABORATORY MICE (*MUS MUSCULUS*) ON FOOD INTAKE AT DIFFERENT TEMPERATURES[1]

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Introduction

Several authors have studied the effects of aggregation upon various physiological processes. Most of the previous work has been done on invertebrates and poikilothermic vertebrates. Only limited studies have been made on warmblooded animals, particularly on small rodents.

The experiments of Vetulani (1931) have demonstrated that the postweaning growth of laboratory mice, as indicated by weight increase, is influenced by the number of animals in the cage. He found that the weight gain of male mice, kept 2 to 4 per cage, was 17.98 percent higher than the gain of mice kept 1 animal per cage; the weight increase of animals kept 9 to 12 per cage was 8.14 percent more than that of those kept 1 to a cage. These studies were repeated by Retzlaff (1939), who confirmed the findings of Vetulani and came to the conclusion that environmental temperature is the main factor causing the difference in weight gain in various population samples. The failure of females to show the same growth response as males, which was observed by both authors, was assigned to peculiarities in female physiology.

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Gerstell (1939) in several experiments has demonstrated that huddling, which tends to conserve body heat, is an important factor in the survival of the bobwhite quail (*Colinus virginianus virginianus*) at low ambient temperatures. Sealander (1952) has studied the effect of huddling on the survival of *Peromyscus* kept at a low temperature without food and water. He found that the survival time of mice exposed to a mean temperature of —23°C was prolonged in groups with 2 to 4 animals per cage, as compared with individually caged animals.

The study of King and Connon (1955) on the effect of social relationships upon mortality in young C57BL/10 mice has shown that the survival of two-week-old animals weighing 7 grams or less depends significantly on proper thermal conditions which may be supplied by other individuals as they huddle together.

The relationship between crowding and food consumption has been studied by only a few investigators. It has been demonstrated by Adolph (1931), that crowded tadpoles consumed less food per animal than isolated individuals. Also the growth rate of the crowded animals was decreased. Kalabuchov (1933, cited by Allee, 1934) has found that individually kept honey-bees eat more

but die earlier than those kept in groups. According to the experimental data of Welty (1934), however, crowded fishes of various species ate more than those kept individually. Yet the growth rate of grouped fishes was slower than of the isolates.

It is the purpose of the present study to evaluate the effect of huddling of laboratory mice on their metabolic rate, as measured by food consumption per gram of body weight. The results obtained at three different ambient temperatures are presented in this report.

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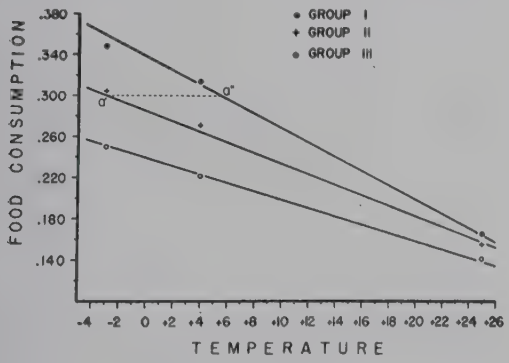

FIG. 1. Relationship between food consumption of MA_f/Sp male mice per gram of body weight and the number of animals per cage at different ambient temperatures (in grams).

MATERIAL AND METHODS

A total of 86 male mice of MA_f/Sp strain were used for the experiments. The animals were housed in stainless steel cages (exterior dimensions: 38 x 23 x 23 cm) with removable sheet metal bottoms. Wooden blocks were placed in each cage instead of bedding, thus eliminating any effect of a nest upon body heat conservation.

At the time of separation of the animals into experimental groups, the food pellets were replaced by powdered food[2] in order to make possible accurate measurements of food consumption. Food was placed in porcelain jars and covered with two pieces of 0.7 cm galvanized mesh wire in order to prevent spillage. The metal screw cap of each feeder had a hole 2.3 cm in diameter in its center. The mice received fresh food every day at approximately the same time. Every individual mouse and the food remains from the previous day were weighed to the nearest tenth of a gram at the time of checking.

[2] Purina Laboratory Chow was used in all instances.

Water was supplied *ad libitum* in self-feeding bottles, which, in the case of mice kept in the Animal Room and in the low-temperature Chamber No. 1, were replaced whenever the level of the water got low. In the low-temperature Chamber No. 2 bottles were refilled daily in order to insure the constant availability of water for the animals.

In order to study the effect of huddling on food consumption of mice at room temperature (the first part of the experiment), the animals were divided into 3 groups: Group I had 1 animal per cage (16 cages), II had 2 animals per cage (10 cages) and III had 5 animals per cage (10 cages). Each of the three population samples was composed of mice ranging in age from 2 to 6 months. The mice were kept in an air-conditioned Animal Room with a constant temperature of $+25°\pm1°C$.

For the study of the effect of low temperatures on food consumption in different groups (the second part of the experiment), each of these original groups was divided into two equal subgroups, each containing animals of comparable ages. One-half of the cages of each group were then placed in a low-temperature walk-in chamber at $+4°\pm1°C$ (Chamber No. 1). At the same time, the other half of the cages were placed in a chamber at $-3°\pm1°C$ (Chamber No. 2). Daily checking of the food consumption and weight of the mice was done outside of the low-temperature chambers. The animals were exposed to normal room temperatures for only one or two minutes at a time.

RESULTS

A period of two days was allowed for the mice to become accustomed to the powdered food. Thereafter, the food consumption was checked regularly for 10 consecutive days. During this time the older animals in all groups maintained their weights at approximately the same level. The younger mice made noticeable gains in weight, showing that access to the food in the feeders was hindered neither by the construction of the latter nor by the presence of other individuals in the cage (groups II and III).

In Table I is shown the effect of the number of animals in the cage on their food consumption per gram of body weight (Column A). The differences between groups were found to be statistically significant ($P < .001$). Since all cages were kept under similar conditions and no fighting occurred in groups II and III during the experiment, the difference in food consumption between groups can apparently be attributed to the

TABLE I. Food consumption of MA_f/Sp Male Mice with respect to the number of animals per cage at +25° ±1°C (in grams)

Group	Number of Observations	A (Mean Food Consumption Per Gram of Body Weight)	B (Mean Food Consumption Per Mouse)
I.....	157	0.166 ± 0.0018*	4.12 ± 0.046*
II.....	100	0.156 ± 0.0020	4.05 ± 0.037
III.....	100	0.141 ± 0.0022	3.82 ± 0.056

*Standard error.

huddling of the mice and to the resultant differences in conservation of body heat.

The data summarized in Column B of Table I illustrate the absolute food requirements of animals in different groups. Here we find a pattern similar to the one in Column A, except that statistically significant differences were found to be only between groups II and III ($P < .01$) and between groups I and III ($P < .001$). The difference between groups I and II was not significant ($P < .3$).

In the second part of the experiment the food consumption at low temperatures was checked for 14 consecutive days in both subgroups of group I, for 8 days in subgroups of II and for 9 days in subgroups of III. Data were not recorded until 48 hours after cages were transferred to the cold rooms. The results for Chamber 1 are summarized in Table II, for Chamber 2 in Table III. The differences between subgroups were found to be highly significant in both Chambers ($P < .001$), except the differences between subgroups II and III in Column B of Table III ($P < .02$).

TABLE II. Food consumption of MA_f/Sp male mice with respect to the number of animals per cage at +4° ±°C (in grams)

Subgroup	A Number of Observations	A Mean Food Consumption Per Gram of Body Weight	B Number of Observations	B Mean Food Consumption Per Mouse
I.....	108	0.314 ± 0.0036*	108	7.72 ± 0.129*
II.....	40	0.271 ± 0.0063	40	6.73 ± 0.153
III.....	44	0.221 ± 0.0035	49	5.71 ± 0.084

*Standard error.

All the mice in Chamber 1 survived during the entire experiment. However, only two out of eight mice from subgroup I survived through the 14 days of checking in Chamber 2. The other 6 animals, including the youngest ones, in this subgroup died within 3 to 13 days after the beginning of the experiment. During several other experiments not connected with the present study, it has been found that under the conditions of the experiment it is impossible to prevent the high mortality of mice kept individually in Chamber 2.

TABLE III. Food consumption of MA_f/Sp male mice with respect to the number of animals per cage at −3° ±1°C (in grams)

Subgroup	A Number of Observations	A Mean Food Consumption Per Gram of Body Weight	B Number of Observations	B Mean Food Consumption Per Mouse
I.....	56	0.349 ± 0.0068*	56	8.85 ± 0.209*
II.....	40	0.304 ± 0.0085	40	7.36 ± 0.254
III.....	39	0.250 ± 0.0067	43	6.55 ± 0.155

*Standard error.

The relatively early elimination of the youngest mice in subgroup I of Chamber 2 (3 to 7 days after the beginning of the experiment) may have influenced the mean value of the food consumption for the whole subgroup, since the youngest animals have shown a tendency toward higher rate of food intake at room temperature. But even if this were true, the food consumption in this subgroup was significantly higher than in the other two subgroups of Chamber 2, and also higher than in subgroup I of Chamber 1.

DISCUSSION

Aggregation, or more specifically, huddling, occurs among some animals as a natural inclination utilized for body heat conservation. It has been called by Brody a "social temperature regulation" (1945, p. 275), and its physiological significance has been indicated by workers cited in the introduction to this report. In addition, Andervont (1944) and Mühlbock (1950) have demonstrated the modifying effects of crowding on the incidence of spontaneous mammary cancer in mice. Both authors have found a higher tumor incidence among females kept individually than among mice confined together.

The experiments outlined in this report shed further light on the efficiency of huddling as a protective factor against heat loss. The results of the study are summarized in Figure 1. There is a general trend toward increased food consumption with lowered ambient temperatures and/or with reduction of the number of animals in a cage.

It is apparent from Fig. 1 (a' a''), that the presence of only one additional animal in the cage can counterbalance the lowering of the ambient temperature for about 8.5°C in the range where this temperature approaches the critical point for the survival of the individually caged animals. In other words, the physiological status of two mice kept together at −3°C, as measured by food consumption, can be compared to the condition of one mouse kept alone at +5.5°C. In these

experiments, survival itself at —3°C was obviously improved by the presence of one additional animal in the cage, as compared with the individually caged mice; none of the animals in subgroup II died in Chamber 2 during the experiment.

It seems to be of particular interest that even at room temperature of +25°C (77°F) the number of animals per cage appears to be an important ecological factor which can bring about quantitative variation in food consumption and possibly other physiological modifications. The number of animals per cage can be an important variable in experimental work.

Summary

The significance of aggregation (huddling) in laboratory mice, as an ecological factor, has been studied at three different ambient temperatures. Food consumption per gram of body weight and absolute food consumption were checked in three groups of MA_f/Sp male mice with 1, 2 and 5 animals per cage in groups I, II and III respectively.

It has been demonstrated that the food consumption per gram of body weight by laboratory mice kept in bare cages varies inversely with the number of animals in the group. As the ambient temperature is lowered there is an increasing divergence in amount of food consumed by the different groups. The data support the hypothesis that crowding is an important ecological factor at lowered, as well as at room temperatures.

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CROWDING AS A POSSIBLE STRESS FACTOR IN INSECT DISEASE[1]

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Introduction

Throughout the literature of insect pathology, as well as that of entomology generally, one finds recurring statements to the effect that excessive crowding or the increased population density of certain insects is likely to cause the outbreak of disease among them. This seems to be true particularly of lepidopterous insects that may become infected with certain bacterial, fungus, protozoan, and virus diseases. Not only does it appear to be true in the case of insects reared in the laboratory, but in populations of insects as they occur in the field (Steinhaus 1954). In nature, disease appears to be essentially a density-dependent factor, and epizootics are most likely at times of high population densities.

The mechanisms by which disease is made manifest in insects as the result of crowding are known only in a vague and general way. It seems likely that in some cases, in certain virus diseases for example, latent forms of the infectious agent are activated. Or, the physiology of the normal defense mechanisms of the insect body are altered or affected in such a manner as to cause the insect to be more susceptible to infectious agents than is ordinarily the case. In other situations, crowding increases the number of direct contacts between

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insects which may increase the rate of transmission of certain infectious agents. In still other instances, crowding increases the concentration of infectious material released by infected insects, thus increasing the opportunity for healthy insects to encounter contaminated food or other objects in their surroundings.

To be sure, it is recognized that in addition to the induction of disease, crowding has other effects on insects as it does on other animals. A commonly accepted generalization in this regard is that by Allee (1931, p. 144):

> . . . we find much evidence supporting the generally accepted dictum that crowding is harmful for poorly integrated groups of animals, breeding and hibernation seasons excepted. We have seen that crowding may slow down the rate of growth and may result in dwarfed individuals, that the rate of reproduction may be decreased, and that the death-rate may be greater. These effects have been reported for so many different animals from such a wide range of the animal kingdom that there can be no doubt of their general significance. But this is not the whole story . . . crowding does not always produce harmful results; and . . . under many conditions there are distinctly beneficial results, providing the crowding be not too great. When considering these beneficial results, we must, however, always keep in mind the harmful effects of overcrowding.

Although it is a frequent observation that the crowding of certain insects in the laboratory often brings about the appearance of disease among them, very little in the way of direct experimentation on this phenomenon has been accomplished. Quantitative data on the subject are almost nonexistent, and little is known of the dynamics involved. The purpose of the present paper is to present preliminary data and associated information which, for the most part, were gathered incidental to other experimentation but which may assist the taking of a small step in the direction of filling this gap in our knowledge.

In the course of our research on the role of certain stressors in the induction of disease in insects (Steinhaus 1957), the factor of crowding became one of primary importance because it affected, directly or indirectly, many of our experiments. In setting up experiments in which living insects are used as test animals, several insects are usually placed together in the same container; at least this is the case in many routine infectivity tests. This immediately introduces the problem of crowding or increased population per unit area, since it is safe to assume that two insects require more room than does one. But the question that naturally follows—how much more room?—is not an easy one to answer. All of which brings us to another basic question: As it pertains to the induction of disease in a given insect species, what constitutes crowding? The results of the experiments reported in this paper probably do not provide any definitive answers to this question, but we hope that they may to some extent clarify the problems involved.

Because precise and understandable terminology is particularly important in papers of this kind, it is well that the reader understands the sense in which we use the word "crowding." Just what constitutes crowding is not generally agreed upon by ecologists and students of population dynamics. Unfortunately, we have found it impossible to reconcile our own understanding of what the word should mean with the varied interpretations found in the literature. Accordingly, we find it necessary to propose a definition which, although we feel it covers the various aspects of the subject treated in this paper, will undoubtedly not satisfy everyone. For our purposes, a simply and purely pragmatic, working definition would be to the effect that, all else being equal, *crowding* is the assembling or forcing of animals into a space smaller than that which they normally require, "demand," or "desire." The effects of crowding would vary according to the influence of other environmental factors. To most people, there is inherent in the word "crowding" the implication that it is a disadvantageous situation; and in everyday usage of the word the author is inclined to accept this implication. Some authorities, however, might consider it inaccurate to define crowding in terms of disadvantage to the animals since, as Allee (1931) has pointed out, increased aggregation of some animals can be beneficial to them. Nor can it be defined only in terms of numbers of animals in a given amount of space since well-integrated groups of species of animals normally aggregate more densely than do those that are poorly integrated. If one removes from the concept of crowding the implication of disadvantage, the term "increased density" would be entirely appropriate except that the word "crowding" is already commonly employed and generally accepted for such situations. The same might be said concerning the concept of the "carrying capacity" of an area with respect to certain animals in nature, but we find it somewhat difficult to apply this idea to experimental situations in the laboratory, such as those discussed in this paper. On the other hand, as far as the dynamics of crowding are concerned, we would concur with Huffaker and Kennett (1956) in equating crowding with an increase in "the intensity of competition for space." To prevent confusion, we prefer to avoid using the term "overcrowding" as used by Allee (1949), since we are not certain that the connotations Allee

gives this word would apply to the situation and data discussed in the present paper.

From a practical viewpoint, there are two types of crowding that may be of importance in the experiments described in this paper. On the one hand, there is the crowding that results from the aggregation of the insects themselves (*i.e.*, different numbers of larvae held in containers of uniform size); on the other hand there is the crowding effect exerted by the size of the container holding the insects (*i.e.*, a constant number of insects in different sized containers). The two are, of course, related and one may be a factor of the other. Nevertheless, it is not always clear at just what point crowding may be said to exist. In other words, in terms of the working definition stated earlier in this paper, it is not always clear at just what point there are more insects in a given amount of space than occur normally in this space. One caterpillar in a greenhouse or a field of alfalfa obviously could not be considered as crowded, nor would it likely be so considered if held in a pint jar. However, if it were confined to a small vial or tight-fitting enclosure, one might consider the insect as being crowded by its physical environment. Or, looking at the matter in a different way, if two insects were confined to a single leaf in the greenhouse or alfalfa field, conditions of crowding (on the leaf) may be said to exist. Whereas in a pint jar the insects, unless confined by the food, may be separated so as to have sufficient room and not be crowded.

In many of our experiments we have used as a container a half-pint paper carton which has a capacity of approximately 14.4 cubic inches (236.2 cc). We have assumed that such a container, holding an adequate supply of food, causes no physical crowding (and hence no stress from crowding) when a single individual of any of the insects used in these experiments is held within it. What may be considered as evidence supporting this assumption is the fact that such individually held insects frequently show no evidence of spontaneous disease[2] at the same time that insects from the same source, but crowded together in the container, do suffer from disease. To complicate matters, however, this is not always the case, since at times the mortality among individually held insects may be rather high, and presumably caused and influenced by factors other than crowding.

It should be pointed out that the experiments herein reported do not include any in which the insects were intentionally exposed to known pathogens during the crowding tests.

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Materials and Methods

It is to be expected that the nature of the results obtained in experiments designed to test the stress of crowding would depend upon the kind of insect involved. Insects (such as ants, bees, silkworms, and the like) that normally live in highly concentrated populations, or in a highly aggregated state, did not appear to us to be suitable animals for such experiments. Accordingly, we used the following species: the alfalfa caterpillar, *Colias philodice eurytheme* Boisduval [Pieridae], the buckeye caterpillar, *Junonia coenia* Hübner [Nymphalidae], and to a lesser extent the variegated cutworm, *Peridroma margaritosa* (Haworth) (= *Peridroma saucia* Hübner) [Phalaenidae] and the California oakworm, *Phryganidia californica* Packard [Dioptidae]. In most of our experiments laboratory-reared larvae of these species were used, although in some instance field-collected material was utilized. As will be explained later, the eggs from which some of the larvae were reared were previously disinfected with 28 percent formalin for 90 minutes.

Unfortunately, the insects just listed were not always readily available in adequate numbers. For this reason the extent of certain experiments had to be curtailed.

In certain experiments, containers of various sizes were used to hold the insects. For the most part, however, the test insects were confined to half-pint paper cartons (Sealright Cylindrical Containers) covered with one half of a glass petri dish. The capacity of this container conforms to that required by the National Bureau of Standards for a half-pint container: 14.4375 cubic inches. However, almost one cubic inch of this space is occupied with food (foliage) and a glass vial containing water to prevent the food plant from wilting. Accordingly, the area available to the insects as determined by the container actually amounted to approximately 13.5 cubic inches.

Most of the experiments described in this paper were conducted at prevailing room temperatures and humidities. Care was always taken that test insects and control insects, in any given experiment, were held under identical conditions. Throughout most of the investigation temperature and humidity readings were recorded by means of

[2] The term "spontaneous disease," as used in this paper, refers to disease that results naturally and from apparently natural causes as distinguished from disease resulting from the artificial injection or feeding of infectious agents.

a hygro-thermograph. The temperatures at which the experiments were performed fell in a range of 21-25°C, usually being maintained at about 22.5°C. The relative humidity of the rooms ranged from 50 to 70 percent, with most experiments being conducted at a relative humidity of about 55 percent. Although temperatures and humidities in the individual cartons were not recorded, it was considered that the variations would be uniform providing the entire experiment was conducted in the same general area within the same room.

The data presented in this paper were submitted to statisticians in the Department of Statistics, University of California, for review. As a result of their consideration of the data, it was decided that the type of descriptive statistics used in the paper was adequate to validate and to explain the principles set forth and the conclusions reached. Since many of the data presented were taken as a by-product from, and at the conclusion of, other experiments being conducted in our laboratory, there was not the opportunity to use an experimental design that provided for a preconceived and detailed statistical approach. Nevertheless, we have been assured of the statistical validity of the data presented insofar as they relate to the conclusions reached, and we recognize the desirability of further experiments along these same lines, the data from which would better lend themselves to a detailed statistical analysis.

Experimentation

Colias philodice eurytheme

Experiments to determine the effects of crowding may be designed in either of two ways, as far as the physical apparatus is concerned. A given number of insects may be placed in each of several containers of different sizes or the size of the containers may be kept constant and different numbers of insects placed in them. However, the degree of crowding is not necessarily proportionate to the total space provided by the container. The extent of crowding is frequently determined largely by the spatial arrangement of the insects' food. If, for example, the food is placed on the bottom of a container, the insects may remain there regardless of the amount of space that may surround the food or extend above it. In the experiments about to be described, both set-ups were used, and notice was taken of situations in which the location of distribution of the food determined the extent of crowding.

Initially Constant Numbers of Larvae in Different-Sized Containers

In a preliminary experiment, 100 larvae were placed in each of five different glass containers having capacities of 10, 69, 147, 658, and 14,112 cu. in. (U. S. inches) respectively. In the case of the last container, the insects were, for the most part, confined to their food (alfalfa foilage) which occupied the bottom six inches of the container, a space of about 2600 cu. in. At the beginning of the experiment the larvae were in the late second instar. All 500 larvae were from the same batch of eggs, and had been reared in small cartons (13.5 cu. in.), about 5 to a carton.

Eighteen days after the beginning of the experiment all the larvae had died in the first three (smaller) containers, and all but one had died in each of the remaining two (larger) containers. In other words, the total number of deaths that occurred in the container that provided 14,112 cu. in. (actually 2600 cu. in.) of space was not substantially less than that occurring in the 10 cu. in. container. However, the rate of death was somewhat greater in the smaller containers, although this difference was greatest between the largest (2600 cu. in.) container and the next largest (658 cu. in.). In the latter, deaths began occurring after the 3rd day, while in the largest container the first deaths occurred on the 9th day. (In another experiment designed along similar lines, generally confirmatory results were obtained using larvae from field-collected eggs.)

There was also a variation as to the cause of death. Larvae dying during the first 8 days of the experiment died of bacterial septicemia as evidenced by the large number of gram-negative small rods present in the blood. Deaths caused by bacteria and/or polyhedrosis virus occurred from the 9th to 12th day. From the 13th through the 18th day deaths were caused almost exclusively by virus infection, although some bacteria were present in preparations made of the dead and dying larvae. It is probable that in the absence of the virus, some mortality caused by bacteria would have been apparent. In any case, the highest mortality occurred after virus infections became apparent (from the 11th to the 16th day).

The results of the experiment just described, raised the question as to what happens to a hundred *Colias* larvae when they are not placed together but are held separately in individual containers. In a sense such a set-up might serve as a control for the experiment already delineated. We were able to make such an observation on 100 larvae held separately (in paper cartons having a capacity of 13.5 cu. in. each) since the 3rd day after hatching. Unfortunately they were from a different batch of eggs than those used in the preceding experiment, but otherwise they were entirely similar.

At the end of 18 days, only 24 of the 100 larvae

were dead as compared with virtually 100 percent of the larvae in the earlier experiment. At the end of 36 days a total of 35 had died; all the remaining had, by this time, become adults. In other words, whereas a virtual 100 percent mortality occurred in the previous experiment in which lots of 100 larvae were held together in the same container, in the experiment in which the same number of larvae were held separately in individual containers the mortality was only 35 percent. (In two other similar experiments using larvae from field-collected eggs, mortalities of 45 and 46 percent were obtained.) The seven larvae that died during the first 8 days had large numbers of bacteria in their blood. In most of the remaining 28, dying between the 8th and 34th days, polyhedra were prominent in all blood smears.

Different Numbers of Larvae Held in Containers of Uniform Size (Half-Pint)

As already indicated, in much of our experimental work, we have found the ordinary half-pint (13.5 cu. in.) paper carton, covered with a petri-dish top, to be a convenient container in which to hold test insects. This container was selected arbitrarily as one in which the effects of crowding could be tested and that could be used in experiments in which the size of the container remained constant but the number of insects varied.

As was revealed by the preceding experiment, when *Colias* larvae were placed singly, together with a supply of food, in half-pint containers, a mortality of approximately 35 percent resulted in the particular lot of insects used. This naturally raises the question as to what the mortality might be if more than one larva were placed in the same size of carton. Accordingly, a series of experiments were set up to ascertain the effects of aggregating 1, 2, 3, 5, 13, 21, and 25 *Colias* larvae in half-pint containers. Unfortunately, different lots of larvae had to be used, but insofar as possible environmental factors such as food, temperature, and humidity were kept constant or within a limited range. With the hope that the results *en masse* might give some idea as to the general effects of crowding, the several experiments and replicates were pooled, and the results are presented in Table I.

Typically, the results indicate that the greater the number of *Colias* larvae held in a uniform size of container, the greater the mortality that occurs prior to the time the insects become adults. In this experiment, the mortality ranged from 32 percent in cartons containing single larvae to 100 percent in cartons containing 25 larvae. It should

TABLE I. Mortality occurring in aggregations of laboratory-reared *Colias philodice eurytheme*. Different numbers of larvae held in uniform size (13.5 cu. in.) container. Summary of several experiments and replicates

No. of larvae per carton		1	2	3	5	13	21	25
No. of cartons		390	103	22	20	3	2	4
Total No. of insects tested		390	206	66	100	39	42	100
No. of deaths		124	93	37	58	31	40	100
Percent of deaths, all causes		32	45	56	58	79	95	100
Percent	Polyhedrosis virus	37	54	30	31	29	10	20
	Bacteria	27	21	62	36	55	75	43
	Microsporidia		2					
	Nonmicrobial (apparently)	36	23	8	33	16	15	37

be mentioned that several additional experiments, not reported here, in which different numbers of larvae were held in half-pint containers, have given similar and confirmatory results.

The exact cause of death of many of the larvae in this experiment is questionable. Certainly, it appears to have been variable. In some cases most of the mortality appeared to be the result of virus activity, in others bacterial activity, and in still others a large percentage of the caterpillars appeared to die of causes unrelated to microbial activity. To what extent any of the mortality was the result initially of stress and secondarily of infection was not ascertained. The theoretical aspects of this matter will be considered in the discussion section of this paper.

That 100 percent of the larvae die when as many as 25 of them are confined to a half-pint container was substantiated by a series of six additional experiments. The data pertaining to these experiments are presented in Table II. In

TABLE II. Mortality occurring in aggregations of *Colias philodice eurytheme* collected from the field as eggs. Summary of six experiments in each of which 25 larvae were held in a half-pint container

Test No.		1	2	3	4	5	6
No. of insects		25	25	25	25	25	25
Instar		3	3	2	2	2	3
No. of deaths		25	25	25	25	25	25
Percent of deaths, all causes		100	100	100	100	100	100
Percent	Polyhedrosis virus	64	60	8	4	24	32
	Bacteria	32	40	64	72	68	64
	Nonmicrobial	4	...	28	24	8	4

each case 100 percent of the larvae (reared from field-collected eggs) died. There are indications that the cause of death in these experiments might, to some degree, be related to the age (*i.e.*, the instar) of the insect. In tests No. 1, 2, and 6, the larvae (at the beginning of the experiment) were in the third instar, and most of these died of virus infection. On the other hand, in tests No. 3, 4, and 5, the larvae were in the second instar, and most of these died of bacterial infection and usually several days earlier than did those dying of virus

infection. We have no explanation as to why there was relatively such a high percentage of deaths from nonmicrobial causes in the case of tests No. 3 and 4.

Many of our experiments on *Colias* were performed with larvae that had been reared in the laboratory for from 2 to 6 generations. In most cases, the eggs from which the larvae hatched had been disinfected with formalin; some had also been held at refrigeration temperatures (*ca.* 4°C) for short periods of time. Accordingly, it was thought wise to run a similar experiment using untreated field-collected eggs directly. The eggs were collected by Carl E. Reiner whose assistance throughout this particular experiment is gratefully acknowledged. Again, the results of this single experiment indicate that the greater the number of *Colias* larvae held in a container of a given size (13.5 cu. in.), the higher is the mortality among them. However, in the cartons containing 1, 2, and 5 larvae each, the mortality was considerably higher than in the corresponding cartons of the preceding experiment using laboratory-reared stock. In the case of the field-collected material the mortality in cartons containing single larvae amounted to 60 percent, almost twice that in the laboratory-reared insects. The mortality rose rapidly to 92 percent when two insects were held in the same carton, and, when 5, 25, or 50 larvae were aggregated, the mortality amounted to 96 percent or more.

On the basis of this single experiment it would be unwise to conclude that laboratory-reared and field-collected insects react significantly differently (in degree) to the effects of crowding, although they do seem to indicate that such is the case, at least in those instances in which one or two insects were held in a carton. On the basis of several years' experience in collecting and rearing *Colias* we have found that ordinarily the mortality among individually held field-collected larvae is considerably less than 60 percent—usually ranging from 5 to 30 percent (Thompson and Steinhaus 1950). Nevertheless, the present experiment indicates what the mortality *can* be in individually held and aggregated larvae from field-collected eggs. Of probable significance is the fact that in the case of the field-collected larvae, 63 percent of the mortality was caused by polyhedrosis-virus infection, whereas of the laboratory-reared larvae only 30 percent died of virus infection. On the face of it, this might indicate that in these experiments the field-collected material contained a greater amount of virus (latent and active) than did the laboratory-reared material.

On occasion, laboratory-reared *Colias* larvae will exhibit a high mortality when as few as two larvae are placed together in each half-pint carton. In one such experiment, we found the mortality to amount to 100 percent as compared with the usual mortality of 45 percent as shown in Table I. Twenty 3rd-instar larvae were placed two to a carton in 10 cartons at room temperature (23°C). All but one were dead at the end of 9 days, and the remaining larva died on the 19th day. Virtually all deaths were caused by a polyhedrosis virus. When this experiment was repeated using three larvae per carton, all of the larvae were dead, primarily of virus infection, in 23 days. Most of the deaths occurred from the seventh to the fourteenth day. Thus it is clear that experimentation of the type being described is subject to a great deal of variation, and that the "history" of the particular lot of insects selected may have a great deal to do with the nature of the results obtained.

At this point it may be well to mention briefly our recognition of the role of temperature in such experiments as these being reported. As indicated in the section on Material and Methods, most of our experiments on crowding were conducted at prevailing room temperatures (21-25°C) and humidities (50-70 percent). Nevertheless, worth citing is one small experiment in which 100 *Colias* larvae were placed in each of two containers of about 58 cubic inches and placed respectively at 45°C (20 percent humidity) and at 23°C (57 percent humidity). A third container of the same size containing only 10 larvae was held at 45°C (20 percent humidity). At the end of four days, 78 percent of the 100 larvae (*i.e.*, crowded) held at 45°C had died; 53 percent of the 100 larvae held at 23°C had died; but of the 10 larvae (*i.e.*, not crowded) held at 45°C only 40 percent died. The exact cause of death was not determined, although most of the dead insects had bacteria in their blood.

Incidence of Disease in Aggregated Larvae Compared with that in Larvae in the Field

During the fall of 1956, a rather interesting contrast was observed between the incidence of disease in *Colias* populations in the field and in larvae collected from the same field but held in half-pint cartons in the laboratory. On September 14, Mr. Reiner collected 700 fourth-instar larvae from an alfalfa field near Winters, California. These were placed in half-pint cartons as follows: 5 cartons containing 50 larvae each, 10 with 25 larvae each, 20 with 5 larvae each, 25 with 2 larvae each, and 50 with 1 larva each. Within 10 days all 700 larvae were dead of polyhedrosis, including the 50 larvae held singly.

On September 25, the same field of alfalfa from

which these larvae were collected was observed again, this time for the presence of obviously diseased caterpillars. Virtually no dead or diseased larvae could be seen in the field upon general observation. When the alfalfa was swept with a net (three 50-sweep samples were taken), 2.5 percent of the larvae exhibited gross appearances of polyhedrosis. Of the apparently healthy larvae collected at this time, 45 were placed in half-pint cartons, 15 to a carton, and by October 4, all had died of disease.

A final check of the field population was made on October 10. By this time most of the insects had apparently pupated or had become adults. In any event, virtually no evidence of disease was seen in the remaining larvae.

It is difficult to know what to conclude from an observation such as this. It would appear that in spite of the apparently low incidence of disease in the field population, enough virus is present in a latent form to cause the caterpillars to manifest the disease when they are brought into the laboratory and confined to half-pint cartons. The fact that even those larvae held one to a carton succumbed to virus infection indicates that all of the increased incidence cannot be explained on the basis of an increased rate of transmission such as might occur under conditions of crowding.

Unfortunately, the manner in which these insects were collected makes it necessary to accept the results with considerable caution. The larvae were swept up by a net, transferred to large paper bags, brought into the laboratory and separated out into the half-pint cartons. This procedure could permit considerable contamination. Nevertheless, because most of the insects died prior to what would have been the entire incubation period of the disease (if contracted at the time of collecting), and because from the time of collecting on, no contaminated food was available to the insects, and because somewhat similar observations were made several years previously in the course of our study of the polyhedrosis in *Colias*, we are inclined to accept the results as at least highly indicative.

Junonia coenia

The *Junonia* larvae used in our experiments were from stock that had been maintained in the laboratory for several generations. All experiments were conducted at prevailing room temperatures (*ca.* 23°C) and humidities (35-50 percent).

Different Numbers of Larvae Held in Containers of Uniform Size (Half-Pint).

In order to gain some idea as to the possible influence of crowding upon the natural mortality of *Junonia* larvae, several experiments were conducted with laboratory-reared insects from eggs that had received the routine formalin treatment. The larvae were placed in half-pint cartons, 1, 15, 25, and 50 per carton. Table III presents the summarized data from these experiments.

TABLE III. Mortality occurring in aggregations of laboratory-reared *Junonia coenia*. Different numbers of larvae held in container of uniform size (13.5 cu. in.). Larvae from formalin-treated eggs. Summary of several experiments

No. of larvae per carton		1	15	25	50
No. of cartons		137	12	12	3
Total No. of insects tested		137	180	300	150
No. of deaths		70	147	281	143
Percent of deaths, all causes		51	82	94	97
Percent	Granulosis virus	89	77	64	55
	Bacteria	1	13	25	27
	Microsporidia	9	9	8	13
	Nonmicrobial	1	1	3	5

As was the case with the *Colias* larvae in a similar experiment, the data of our experiments with *Junonia* show that the greater the number of larvae confined to a given space, the greater is the percent mortality. With the particular lots of insects used, 51 percent of the individually-held larvae died of infection, 82 percent of the larvae held 15 to a carton similarly died, as did 94 percent of the 25 per carton group and 97 percent of the 50 per carton group.

Most of the deaths were caused by infection with a granulosis virus (*Bergoldia lathetica* Steinhaus). This was especially marked in the 1 and 15 larvae per carton groups where the virus-caused mortality amounted to 89 and 77 percent respectively, as compared with 1 and 13 percent associated with bacterial activity, and 9 percent in each case associated with the presence of microsporidia. In the 25 and 50 larvae per carton groups the percentages dropped to 64 and 55 as far as virus mortality was concerned and the bacterial mortality rose to 25 and 27 percent respectively. Microsporidia were observed in 8 percent of the dead larvae in the former group and 13 percent in the latter group. From the standpoint of cause of death in this experiment, therefore, it would appear that the percentage of deaths associated with virus activity decreases, and the percentage of deaths associated with bacterial activity increases, as the number of larvae held in the half-pint containers is increased.

It will be noted that the mortality percentage in the case of the individually held *Junonia* larvae (51 percent), is somewhat greater than among similarly held *Colias* larvae (32 percent). Whether or not this is a true difference is difficult to say. Of possible significance in this regard is

the fact that in the course of our investigation we have observed small groups of individually-held *Junonia* larvae in which no deaths whatever occurred, a circumstance found less often with *Colias* larvae. For example, 16 randomly selected *Junonia* larvae (individually held in half-pint containers) were observed daily until they became adults. During this time not a single death occurred, whereas from the same lot of insects 20 percent of the larvae died when held two per carton, 56 percent died when held five per carton and 97 percent died when held 25 per carton. (We have found certain lots of individually held, apparently healthy, *Colias* larvae to experience mortalities of up to 60 percent.)

Different Numbers of Larvae Held in Small Containers of Uniform Size (1.5 cubic inches)

When *Junonia* larvae were held individually in very small containers (*i.e.,* in small glass Petri dishes enclosing 1.5 cubic inches of available space), the mortality percentage was significantly higher than was the case with *Junonia* larvae held individually in half-pint (13.5 cubic inches) containers. In one experiment, for example, 21 *Junonia* eggs were placed singly in the small Petri dishes. Five of these eggs failed to hatch. Upon hatching each of the remaining 16 larvae were provided with food (plantain) and observed daily for evidence of disease and for mortality. No deaths occurred in any of the 16 larvae for the first three instars; one larva died of a combined bacterial and virus infection in the fourth instar. However, 14 of the remaining larvae died in the fifth instar (13 of granulosis virus and one of bacterial infection), while the one remaining insect pupated and emerged as an adult. In other words, of the 21 original individually held specimens, all but one died before becoming adults. Of those that died, 25 percent died as eggs, 5 percent died in the fourth instar and 70 percent died in the fifth instar. (Considering the larvae alone, 94 percent died in the fifth instar.) As to the cause of the deaths, the eggs apparently just failed to develop although it is possible that some of them were injured in handling. Of the 15 dead larvae, 93 percent died of granulosis virus infection, and 7 percent died of bacterial infection. Concerning the matter of larval mortality alone, the fact that 94 percent of the larvae died as compared with 51 percent of those held in half-pint containers (see Table III) may be of significance even considering possible inherent difference in the two lots. Since, in this experiment, there was no opportunity for transmission of virus from one individual to another, the insects either must have been uniformly contaminated in the egg stage, or they were uniformly carrying latent virus. Whether or not the disease was activated because of the stress of crowding in the small 1.5 cubic inch container (the available space of which naturally decreased as the larva increased in size) as compared with the conditions afforded by the half-pint (13.5 cubic inches) container cannot be proved by these data, but the indications are that this is the case. If latent virus was not involved, it is possible that the eggs may have harbored or been contaminated with virus, infecting the larva upon hatching. However, the eggs had been treated with 28 percent formalin to disinfect their external surfaces. (As pointed out elsewhere, however, this does not mean that the larvae from such eggs are any less prone to disease.) Furthermore, most of the larvae died approximately 45 days after hatching. Since, ordinarily, death results from 6 to 12 days after infection (Steinhaus and Thompson 1949), it does not appear likely that infection began at the time of hatching. More likely, perhaps, is the possibility that sometime during the development of the larvae, perhaps during the late 2nd, 3rd, or 4th instars, virus latent within the insect became active giving rise to the disease which killed the larvae in the 5th and last instar. Possibly, as the larvae increased in size, a point was reached at which the stress factor triggered the virus into activity.

Effects of Crowding Using Colias *and* Junonia *Eggs Not Treated with Formalin*

Beginning in 1949, all the eggs used as a source of laboratory stock were routinely immersed in 28 percent formalin for 90 minutes, followed by a 15-minute aqueous rinse, for the purpose of sterilizing their surfaces and thus decreasing the chance of the hatching larvae becoming infected through external contamination. Especially was this treatment thought to be effective in inactivating viruses. In the case of *Colias* we found this treatment to yield 98 percent disease-free larvae as compared to 65 percent disease-free larvae from untreated eggs (Thompson and Steinhaus 1950). Subsequent experience, however, indicates that this procedure does not yield invariably uniform results. Although it may have disinfected the eggs, there are indications that this treatment may at times cause the larvae from such eggs to be more prone to disease than are larvae from untreated eggs.

In one small experiment with *Colias,* for example, untreated eggs from the same stock as the treated eggs used in the experiments from which the data in Table II were compiled, showed considerably less mortality when held one or two per carton. Ten larvae from untreated eggs held one

or two per carton showed only a 10 percent mortality as compared with 32 percent mortality in the case of the treated eggs; those held two per carton showed 27 percent mortality as compared with 45 percent when the larvae were from treated eggs. However, it must be admitted that we have seen a great deal of variability in the mortalities of similar lots of *Colias* larvae that we have reared during the past several years.

In the case of the *Junonia* larvae used in the present experiments, fewer deaths occurred in larvae from untreated eggs than from eggs that had been immersed in formalin. The data pertaining to the untreated insects is presented in Table IV; these may be compared with the data

TABLE IV. Mortality occurring in aggregations of laboratory-reared *Junonia coenia*. Different numbers of larvae held in container of uniform size (13.5 cu. in.). Larvae from eggs not treated with formalin

No. of larvae per carton		1	2	6	9	10	15	50
No. of cartons		18	4	2	1	1	4	3
Total No. of insects tested		18	8	12	9	10	60	150
No. of deaths		2	3	6	2	4	34	95
Percent of deaths, all causes		11	38	50	22	40	57	63
Percent	Granulosis virus	50	33	67	50		35	38
	Bacteria	50		33	50	25	24	40
	Microsporidia						12	9
	Nonmicrobial		67			75	29	13

relating to the treated insects given in Table III. Although the original numbers of insects used in the experiments concerned varied, it may be noted that larvae from the untreated eggs held one per carton showed a mortality of only 11 percent, while similarly held larvae from treated eggs showed a mortality of 51 percent. Those larvae held 15 per carton showed 57 percent mortality (untreated) as compared with 82 percent (treated); when held 50 larvae per carton the mortality was 63 percent (untreated) as compared with 97 percent (treated).

Without additional experimental evidence it would be presumptuous to interpret these results as the effects of stress brought on by the formalin treatment. Nevertheless, this is a distinct possibility. The formalin treatment is known to reduce the number of eggs that would ordinarily hatch (see Thompson and Steinhaus 1950), so evidently the procedure is a rigorous one. That a "weakening" effect can carry over to the larvae hatching from the eggs that do survive can only be a speculation as far as can be discerned from the data and information available.

Peridroma margaritosa and Phryganidia californica

Most of our crowding experiments using *Peridroma* larvae were thwarted by the fact that these insects at times are markedly cannibalistic. Ordinarily cannibalism may occur when more than two or three are aggregated; we have found a considerable amount of cannibalism to occur when more than 15 are grouped together in a half-pint container. In spite of the difficulties caused by cannibalism, however, sufficient data have been obtained to indicate that, as with *Colias* and *Junonia*, the greater the number of *Peridroma* larvae confined to a given space, the greater is the mortality percentage. Virtually no deaths occurred when the larvae were held 1 or 2 to a half-pint carton. When held 5 per carton, 20 percent of the larvae died; when held 15 per carton, 60 percent of the larvae died. The cause of the mortality appeared to be about equally divided between virus, bacterial, and nonmicrobial.

As evidenced by a single experiment, the general phenomenon of a higher mortality occurring the greater the number of larvae held in a given size of container appears to apply to the California oakworm (*Phryganidia*), although this may not be apparent in aggregates of below 25 or 50 in half-pint containers. When 1, 2, 5, 25, and 50 larvae respectively were held in half-pint cartons, the mortality began at about 4 percent with the individually held larvae, and did not rise appreciably until it rose to 15 percent among larvae held 50 to a container. About 43 percent of the deaths were caused by a polyhedrosis virus, 7 percent by bacteria, and 50 percent by undetermined causes. The data from this single experiment indicate that the phenomenon holds true but to a less intense degree than is the case with the other species studied.

Nature of Pathogens

From the foregoing account it will be noted that the kinds of diseases most frequently induced were those caused by viruses, bacteria, and occasionally protozoa. No instances of induced fungus diseases were noted. This is as might be expected mainly because of the nature and methods of transmission of fungus infections in insects and the dependence of these microorganisms on large amounts of moisture in order to initiate infection.

In the case of the viruses, that occurring in *Colias* larvae was the polyhedrosis virus *Borrelina campeoles* Steinhaus; that in *Junonia* larvae was the granulosis virus *Bergoldia lathetica* Steinhaus;[3] that in *Peridroma* larvae was the granulosis virus *Bergoldia daboia* Steinhaus; and that in the

[3] Weiser (1958) has recently designated this species as *Steinhausia lathetica* (Steinhaus), the type species of a new genus.

Phryganidia larvae was the polyhedrosis virus *Borrelina peremptor* Steinhaus.

A larva was diagnosed as being infected with or having died from a bacterial infection when an examination of its blood or its body cavity showed large numbers of bacteria to be present. In most cases it was assumed that these bacteria had caused or contributed to the death of the insect by virtue of the septicemia they had produced. In only a few instances were the bacteria identified as to species. In general, it was found that the bacteria concerned were gram-negative short rods, some of them fermented lactose (*i.e.* were coliforms) while others did not. They appeared to be of the type ordinarily, or at least occasionally, found in the alimentary tracts of the insects. In only rare instances were sporeformers detected that could have been considered the cause of death.

On the few occasions when protozoa were found causing the mortality, they were identified as Microsporidia. In these cases species identification was not attempted.

When careful microscopic observations of the dead insects showed no visible microorganisms of any kind, the deaths were designated as "non-microbial."

Incidentally, throughout the experiments reported in this paper, it was recognized that the cause of death might vary according to a number of factors. For example, it is undoubtedly true that some of the insects dying from bacterial infection early in an experiment would, had they lived, have died later of virus infection.

Discussion

It has been our experience that the type of experimentation and results reported in this paper are characteristically difficult to interpret, and we must, therefore, straightforwardly admit to an inadequacy in this regard. Nevertheless, it appears worthwhile to consider the possible significance of our findings to date, and to attach to them the qualifications requisite for the valid interpretation of such preliminary data.

At this point it is well to review briefly some of the variables which undoubtedly affect the experiments that have been reported in this paper. Of paramount importance, for example, is the history of the insects prior to the time they were used in the experiments. Such matters as the storage of eggs or larvae in the refrigerator, treatment of eggs with formalin, and the extent of crowding during early instars have been recognized as factors capable of influencing the results of many of the experiments we have conducted, but other experiments and appropriate controls, have been performed to account for them.

More difficult to account for, however, is the effect on the insects (in any crowding experiment) of the decrease in the numbers of insects through death. In other words, in an experiment designed to test the effects of crowding on, say, 25 insects held in a given container, ten insects may die (and be removed) during the early days of the experiment so that actually the test, for most of its duration, involves only 15 insects. Or the deaths may occur gradually and regularly so that there is a decreasing number of insects in a situation becoming decreasingly crowded. To some extent the reverse may also occur. That is, as an experiment progresses the larvae naturally increase in size, taking up more of the available space, and thus presumably intensifying the crowding effect.

The matter of determining the exact amount of space available to insects within a container of a given size also presents a problem, especially since the spatial factor is a relative one. Since the larvae with which we worked could not suspend themselves freely in space, such space could not, strictly speaking, be considered as available to them. Instead the larvae availed themselves of the space in two dimensions: *i.e.*, that available to them on the surface of the walls and floor of the container and on the surface of the food plant. If the bouquet of food (*e.g.*, alfalfa sprigs) was bushy and leafy, it would provide more surface space for the insects than would a bouquet not having these characteristics. Therefore, to say that a given container provided 13.5 cubic inches of space for a given number of insects is correct only insofar as the total amount of this space is utilized by insects on the food plant and on the walls of the container.

The design and conduct of our experiments were to some extent dependent upon the supply and condition of insects available at the time. Unfortunately, comparisons occasionally had to be made between groups of insects reared at different times and from different egg masses. In some cases the comparison or combination of data from these different lots provided a sort of "average" which has value in providing certain generalizations. In other instances, the preciseness of the data would have been enhanced if comparisons could have been made between insects from the same egg mass. In any event, the routines of procedures and techniques used in rearing the insects in our Laboratory are well regulated and standardized, and provide a generally uniform and satisfactory standard of quality of stock insects.

As far as the objectives of the present investigation are concerned, a crucial point in interpret-

ing the results concerned itself with how well the stress of crowding was separated and held distinct from other factors and other stressors. In most of the experiments, did disease appear as the result of, or was it triggered by, the stress of crowding as determined by metabolic or physiological changes in the insects, or was it a reflection of increased transmission of the pathogens from one insect to another as may occur under crowded conditions? Or did the fact that in some of the experiments the frass of the insects was not removed from the containers, itself constitute a stress or provide a means of contaminating healthy larvae? These possibilities were recognized from the start of our investigation and control experiments were designed with the hope of accounting and compensating for them. For example, as concerns the latter question, the matter of clean versus frass-contaminated containers was clarified with respect to *Colias* and *Junonia* by direct experiments. Parallel crowding experiments were run using on the one hand containers cleaned, changed, and sterilized daily, and on the other using containers in which the frass was allowed to accumulate throughout the course of the experiment. In general, no significant difference could be detected in the larvae or in the results of the experiments conducted using the clean as distinguished from the frass-contaminated containers.

The results of the present investigation have been clear in at least one respect: the greater the number of insects held, or "crowded," together in a container of a given size, the greater is the number that die of disease. In some instances it appears that the effect of crowding may be that of providing greater opportunity for the transmission of infectious agents from one insect to another, or from contaminated frass and debris to healthy insects. On the other hand, there is evidence that the effect of crowding may also be that of reducing the resistance of the larvae to latent pathogens or to microorganisms normally in the environment. If this happens, it could be brought about through changes or alterations in the insects' metabolism or general physiological responses.

The evidences of which we speak are of three types:

(a) In some experiments the disease (virus) first appears so long after the beginning of the experiment that had it begun through contamination or transmission from the preceding generation, the incubation period of the disease would long since have lapsed. Transmission from diseased to healthy insects does not appear likely since in these experiments the deaths of virtually all the insects occurred at about the same time. The most ready explanation for the results obtained is that the virus was latent in the insects and manifested itself only after a relatively long period of stress. That the stress involved was crowding appeared likely since insects held separately, and presumably not under stress, did not show the high mortality that occurred among the crowded individuals. Furthermore, we have found experimentally that transmission by direct contact does not normally occur under the circumstances prevailing in these experiments or during the periods of larval life concerned.

(b) In another part of this general investigation, we have obtained experimental evidence that larvae suffering from virus infection (particularly in those instances where the virus develops in the tissues of the body cavity) do not liberate virus along with their body wastes, at least not until late in the disease, or until the breakdown of the gut epithelium. Accordingly, virus transmitted in this fashion would not be responsible for infection in those instances where the disease occurs early in the crowding experiment. In such cases, it would appear that the effects of the stress induced the appearance of the disease before transmission by contact could occur.

(c) Although the restraining of an insect with inanimate, solid objects may be quite a different situation than insects crowding each other, it is interesting that in a few experiments in which physical crowding was tested results were obtained similar to those obtained when the insects themselves were crowded together. When *Colias* larvae were retained in "straight jackets" between glass slides (with food available to them), or when individual larvae were held individually in narrow glass tubing, they showed approximately the same percentage of mortality (80 percent) as did larvae held 15 to a half-pint container.

Summary and Conclusions

1. This paper describes an attempt to investigate, in a preliminary way, the effects of crowding on the occurrence of disease in certain lepidopterous insects. The insects used were the larvae of *Colias philodice eurytheme* Boisduval, *Junonia coenia* Hübner, and to a lesser extent *Peridroma margaritosa* (Haworth) and *Phryganidia californica* Packard. Depending upon the experiment, both field-collected and laboratory-reared specimens were used.

2. A large part of the data was gathered from experiments designed for purposes other than that of testing the effects of crowding. From the standpoint of the present report, however, the nature of the experiments was such as to test the effects of crowding in half-pint paper cartons in which

different numbers of insects were placed. The experimental methods and procedure varied considerably. A large amount of data was gathered, condensed, tabulated, and broadly analyzed. Statistical analysis was limited to that of descriptive statistics. Within the limitations of the experiments, and considering the difficulties involved in interpreting the data, the following general conclusions are offered on a tentative basis:

3. With poorly integrated species of insects it appears that conditions arbitrarily acknowledged as constituting crowding tend to induce the appearance of disease among insects under such conditions. In other words, crowding of certain insects increases the incidence of disease among them. (This generalization probably does not apply, or applies to a lesser degree, to spatially well-integrated species of insects.) Some of almost any group of larvae held individually and uncrowded may succumb to disease, but this percentage mortality is almost invariably significantly lower than that which occurs among aggregated and crowded larvae.

In general, the greater the number of larvae held in a container of a given size, the greater the mortality that occurs prior to the time the insects become adults. The mortality rose to 100 percent as the numbers approached 25 larvae per half-pint carton. However, varying amounts of mortality occurred among larvae held one to a carton—an arrangement not considered to constitute crowding.

4. That the disease is induced or the pathogens activated by the stress effects of crowding is not entirely certain, although indications are that such is the case. In some situations the disease seems to appear as the result of the activation of latent virus. In other cases, it appears that because of the stress of crowding the resistance of the host is lowered to a point where microorganisms normally present in the environment (including the insect's alimentary tract) are able to invade the body cavity of the host and cause disease. These situations appear to occur in addition to, but at times distinct from, the transmission of pathogens from one insect to another as it may occur under conditions of crowding.

5. The kinds of diseases most frequently induced by crowding in the particular lepidopterous insects studied (especially in larvae of *Junonia* and *Colias*) were those caused by viruses, bacteria, and occasionally protozoa (Microsporidia). The bacteria appeared to be of the type ordinarily or occasionally found in the alimentary tracts of the insects concerned.

6. Usually the effects of crowding are first manifested within a week as far as bacterial disease is concerned, and within 8 or 10 days as far as virus disease is concerned. However, there is considerable variation in this respect, and sometimes the effect appears to be delayed. Commonly, deaths occur over an extended period covering the entire larval and pupal life of the insect.

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SOME FEATURES OF THE RELATION OF INSECTS TO THEIR ECOSYSTEMS

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One of the most difficult problems in entomology is to find out how the abundance of insect pests is controlled in nature. We know something about its general features, but we do not often know why a particular pest is abundant in some areas but not in others, or why outbreaks occur in one year and subside in the next, although many of the major pests have been under investigation for twenty years or more. Entomologists have been arguing heatedly during this time over the relative merits of chemical and biological control, but there is still no way of determining which method will be the most successful against a particular species except by trial and error.

In parasite introduction there are elaborate and efficient procedures for collecting, shipping, rearing, releasing, and recovering introduced species, but no method of determining in advance which, if any, can be successfully established or what ecological niche a successful enemy may be expected to fill.

When a new insecticide is recommended for public use, the entomologist who recommends it seldom has more than a vague idea of how it will affect the natural enemies of the pest or the enemies of other pests. In other words, when applied control becomes involved with natural control, the investigator is generally compelled by the lack of information to proceed on an empirical basis.

The chief difficulty is, of course, the inherent complexity of the relations between a pest and its environment. The factors controlling the abundance of a pest may be numerous and are nearly always obscure. The need for more basic information is recognized by nearly everyone, but few investigators make more than piecemeal attempts to obtain it. It is generally assumed that a reasonably complete understanding of how a pest is controlled in nature would require so much research that the undertaking is impractical. This paper will challenge this assumption and examine the problem in the light of the prevailing theories of natural control and with the help of some data obtained in the course of an investigation of the biology and control of the green peach aphid (*Myzus persicae* (Sulz.)) and the hornworms (*Protoparce sexta* (Johan.) and *P. quinquemaculata* (Haw.)) that attack tobacco. The work was done in cooperation with North Carolina State College and the North Carolina Department of Agriculture.

Theories of Natural Control

Differences in meaning of the word "control" have been the cause of much confusion in the literature. In this paper the word refers to any factor that has a significant effect on a population, regardless of whether the effect is positive or negative, direct or indirect, or whether it causes the population to vary or tends to stabilize it.

The early investigators of natural control proposed rather simple explanations. Thus, Howard and Fiske (1911) suggested that the most important factors controlling populations were natural enemies, particularly parasites. Bodenheimer (1930) rejected this hypothesis and held that weather was the most important variable determining insect numbers. Later, both sides of the controversy modified their positions to take account of the evident fact that both weather and biotic factors had profound effects on populations. Smith (1935) held that weather might cause populations to vary, but only density-dependent factors, which are mostly biotic, can prevent the extermination of a species and are chiefly responsible for limiting and stabilizing numbers. Bodenheimer (1938) agreed that at high population levels biotic factors caused reductions in numbers, but he continued to insist that at normal levels weather was of paramount importance. Judging from the literature, most entomologists primarily interested in chemical control would probably agree with Bodenheimer, and those interested in biological control would agree with Smith.

Another line of thought that has a bearing on this whole problem was developed primarily by ecologists. Clements and Shelford (1939) used the word "biome" to describe the whole interconnected complex of plants and animals inhabiting a region. Tansley (1935) used "ecosystem" to include the physical environment in this complex. "Ecosystem" was defined by the Committee on Nomenclature of the Ecological Society of America (Eggleston *et al.* 1952) as "the community (its component organisms, the habitat and the eco-climate all considered together as a unit."

Most entomologists who have recently discussed ecological theory accept Smith's hypothesis that the stabilizing and limiting factors are density-

dependent variables, but emphasize the complexity of the factors controlling insect abundance. Thus, Solomon (1949) says "A population and the items of its environment form a closely interconnected complex or ecosystem. The relationships of a population are with the whole ecosystem (which includes itself) rather than with the environment only. . . . The level of abundance depends ultimately on all the major elements of the ecosystem, although the density-related, controlling factors are the immediate determinants."

In this brief account of ecological theory the principal hypotheses have been oversimplified and many important concepts have been ignored for the sake of brevity. A much more comprehensive review can be found in Solomon's paper. The significance and limitations of these concepts can best be discussed in relation to a specific pest.[1]

Green Peach Aphid Complex in North Carolina

The seasonal sequence of populations of the green peach aphid at Oxford, N. C., is shown in Figure 1. In North Carolina this aphid is active

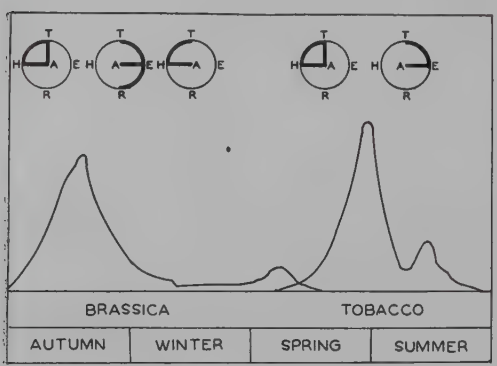

Fig. 1. Seasonal cycle of populations of the green peach aphid in North Carolina. Heavy lines in the circles indicate major interactions between factors. H, hosts; E, enemies; T, temperature; R, rainfall; A, aphids.

throughout the year, and no sexual generation has been found. The important hosts are species of *Brassica* in the winter and tobacco in the summer. The steep rise in populations in the fall occurs at a time when the host plants are young and in good condition, temperatures are favorable, and there are very few natural enemies. The drop in populations early in the winter is caused by a fungus disease of aphids, which begins following the first heavy rain in cool weather and is associated with low temperatures and a continuously wet soil under the plants. Further decreases in the winter occur when the host plants are killed or badly injured by frost. The aphids themselves were not killed by the lowest temperatures in four years, but the hosts were frozen.

In spring the fungus subsides with the coming of warmer and drier weather and there is a short period of aphid increase on the winter hosts, which is cut short by host maturity or removal. The increase on tobacco is again associated with young growing hosts, favorable temperatures, and few enemies. In June or July, when temperatures reach 90°F for several days in succession, there is a very heavy mortality. It has not been definitely determined whether this is due to a pathogen or to some effect of temperature on the host plant, but the evidence favors a pathogen and is strongly against a simple temperature effect. For instance, heavy mortality may occur on some plants as much as a week earlier than on others nearby and may be delayed by the removal of dead aphids. Populations may again increase in a period of cooler weather, but disappear as the plants reach maturity.

The only weather factor that has a significant direct effect on mortality is heavy rainfall accompanied by high winds. Such storms may remove as much as half the population, but such losses are infrequent and temporary and are hardly comparable to the steady attrition of disease. Although temperature apparently has no direct effect on aphid mortality, it does have marked effects on the rate of reproduction and on the host plants and diseases.

The initial populations on tobacco depend on the winter survival and the proximity of winter hosts. In most of the State, economic infestations of plant beds can be prevented by destruction of nearby winter hosts. The amount of damage to tobacco in the field depends on the initial infestation and the time available for increase before hot weather begins. The most injury occurs in fields with high initial infestations in years when the incidence of 90°F temperatures is late. This relationship also determines whether or not insecticides will be needed and when they should be applied (Lawson and Chamberlin 1957).

A comparison of these data with the general theories of populations reveals some important discrepancies. Bodenheimer (1938, p. 111) says: "Under normal conditions climate really controls population density in being responsible for the highest degree of destruction." Obviously this statement is not true of the green peach aphid.

[1] A review of more recent population theory can be found in "Population Studies: Animal Ecology and Demography." Cold Spring Harbor Symposia on Quantitative Biology, Vol. XXII. The Biological Laboratory, Cold Spring Harbor, N. Y. 1957.

The highest degree of destruction is caused by biotic factors. Even the effect of rainfall in washing aphids off the plants is complicated by the biotic factor of size and position of leaves on different hosts. However, changes in populations are initiated by changes in weather. For example, neither the winter decline nor the spring increase would occur without the change in weather. Temperature or rainfall, or both, is ultimately involved in every major change in population.

Smith's generalization that density-dependent factors determine the "steady density" of a population and damp its fluctuations also has limitations. Host density, no doubt, has some effect on the rate of mortality from disease, and the rather constant population for long periods in the winter may be a "steady density," but density effects alone do not explain the population phenomena any more than weather alone will explain them. For example, the time and place where fungus disease causes heavy mortality are not determined primarily by density but by weather. Aphid numbers on tobacco in the spring are determined mostly by the location of winter hosts, and the peak population on the crop depends on the incidence of high temperatures. Neither of these variables is in any way related to aphid density. In brief, none of the theories that assign a paramount role in natural control to a particular type or class of variable will explain the population dynamics of the green peach aphid. If the investigations of this pest had been limited to weather, biotic, or density-related variables, much significant and useful information would have been missed.

The ecological hypothesis that insects are controlled by the whole ecosystem seems to be a much more realistic concept than the earlier ideas. If each of the major changes in population is considered separately, no two of them involve exactly the same set of factors and each is the result of an interaction between the aphid itself, a weather variable, and either a host plant or an enemy (Fig. 1). Not only does each of the interactions involve at least three major elements of the ecosystem, but it also involves other minor factors. For example, the reduction in aphid populations due to host-plant injury from low winter temperatures is on the surface a rather simple interaction. The host plants are killed or injured by frost and the aphids die from lack of food. Actually this effect involves numerous other factors. Temperature also determines the ability of the aphid to move from injured to healthy plants. Soil moisture and fertility, plant density, age, and previous condition, and other insects no doubt affect the amount of injury to host plants and recovery in the spring. If all the factors having any effect on the aphid are considered, the control of populations is a very complex matter indeed. In this sense it is perfectly true that aphid populations are controlled by the whole ecosystem.

The characteristic interactions between the green peach aphid, its hosts or enemies, and weather, are typical of many other insects. Similar interactions were demonstrated for the pale western cutworm by Cook (1930) and Seamans (1923), for the Angoumois grain moth by Simmons and Ellington (1933), and for the wheat stem maggot by Rockwood, Zimmerman, and Chamberlin (1947).

Limitations of the Ecosystem Concept

Although the concept that insect populations are controlled by the whole ecosystem is closer to the facts of nature than previous ideas, this concept also has certain limitations. Whereas previous ideas erred on the side of oversimplification, the ecosystem concept is too broad. Although it is true that a large number of factors have some effect on the green peach aphid and interact in an intricate fashion, most of these factors are of little significance. For practical purposes the abundance of the aphid in the vicinity of Oxford is determined by eight variables. These are temperature, rainfall, four host plants, and two natural enemies, both of which are diseases. None of the numerous species that compete with the aphid for food and none of the other enemies of aphids or the alternate hosts of the two diseases are of any real significance, except locally and occasionally. Furthermore, the limited information available from Florida, Georgia, Tennessee, and Maryland indicates that the same factors control aphid abundance in those areas except that there are one or two additional host plants.

The relatively small number of variables mentioned above is in part a matter of classification. Factors such as humidity, which is a product of temperature and rainfall, and length of day, which has a constant effect on host-plant maturity, have been arbitrarily omitted. The only remarkable feature is the small number of hosts and enemies. In theory the aphid could have 20 or more host plants and as many enemies, all of them important. Actually there are at least that many hosts in the Oxford area, but only four are sufficiently abundant to be of any real significance. The total number of enemy species is not known, but there are at least five species of parasites and three families of predators in the United States. The hosts are cultivated crops or weeds, which are more or less under the control of man who may suppress some and favor others, but there is no

apparent reason why the number of significant enemies is limited to two diseases. Some of the parasites and predators are very common insects, but they do not have much effect on the aphid.

This limitation on the number of enemies is not just a matter of relative importance where one enemy, for example, takes 30 percent, another 20, and so forth. The differences are of much greater magnitude. The loss to parasites has been measured. It is about 3 or 4 percent compared with losses to disease of about 99 percent. The take of predators has not been measured, but cannot be more than a small fraction of the kill by disease.

The fact that the number of hosts or enemies is limited to two or three significant species is of great significance if it is generally true of other insects. If the investigator can expect that the hosts and enemies of any pest will be limited, then his task of unraveling the complexities of ecosystems will be greatly simplified. Whole ecosystems are completely unwieldly units for either study or manipulation. The number of factors involved is too great, and too many of them cannot be controlled.

The literature indicates that most pests of plants have no more than three or four significant hosts. However, most of the well-known species attack agricultural crops, which are artificially abundant. A few species that have wild host plants do show the limitation. Lawson and Piemeisel (1943) found that the beet leafhopper (*Circulifer tenellus* (Baker))in California had only three summer hosts that were sufficiently abundant to have an important effect on populations although a number of other species were good hosts. According to Benjamin (1955), 22 plants are attacked by the red-headed pine sawfly (*Neodiprion lecontei* (Fitch)), but oviposition occurs on only nine species and no more than three of these in the same State.

Adequate data on the natural enemies are available for only a few species. Hamlin *et al.* (1949) found that the alfalfa weevil (*Hypera postica* (Gyll.)) has only one significant enemy during the active season. Varley (1947) found that most of the mortality of the knapweed gall fly (*Urophora jaceana*) was due to caterpillars, mice, and one parasite; there were four other parasites of doubtful importance.

The wheat jointworm (*Harmolita tritici* (Fitch)) is attacked by at least five parasites in Oregon, but two of them account for over 95 percent of the total parasitism (Chamberlin 1941). Benjamin (1955) states that 58 species of parasites and predators and at least one disease attack the red-headed pine sawfly, but in studies in Illinois he found that one egg parasite destroyed from 80 to 100 percent of the population and one larval parasite over 75 percent of the remainder.

Most authors give a long list of enemies of insect pests with little indication of their relative take. A few investigators indicate that one or two enemies are much more abundant than others, but these are generally parasites that are easy to see and the predators are often ignored. Thus, nearly all the work on the enemies of insects is incomplete.

In the absence of adequate experimental data another approach to the problem is necessary. If it can be shown that there is some inherent limitation to the number of enemies attacking a given host, then it can be inferred that this limitation would apply to others. In the case of the green peach aphid the reason for the limitation is not apparent, but a study of the enemy complex of the tobacco hornworm shows certain principles of organization that would have a limiting effect.

Natural-Enemy Complex of the Hornworms on Tobacco

In North Carolina *P. sexta* is far more abundant than *P. quinquemaculata,* and most of the observations given below apply to the first species. Tobacco is the only important host. The eggs are laid on the leaves, and the larvae feed on the lamina and smaller veins. There are usually five larval instars. Pupation occurs in the soil, and there are three distinct broods each year (Metcalf 1909). The major enemies are named in Figure 2, which also shows the instars attacked.

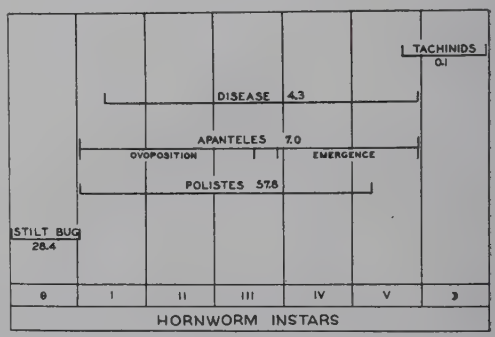

Fig. 2. Natural-enemy complex of the tobacco hornworm. The numerals are percentages of the number of eggs laid that were destroyed by each enemy. Survival to the pupal stage was 2.2 percent, and 0.2 percent was lost from miscellaneous causes.

The stilt bug (*Jalysus spinosus* Say) is an important egg predator. Two species of *Polistes, P. fuscatus* (F.) and *P. exclamans* Vier., kill most of the larvae. Several other predators, such as the spider *Peucetia viridans* (Hentz), nabids,

Geocorus sp., and birds have been seen to attack hornworms, but only infrequently. Cage experiments and close observation of small plots indicate that only the wasps and stilt bugs kill appreciable numbers. Thus, three species of predators kill about 80 percent of the hornworm population. These three plus the parasite *Apanteles congregatus* Say kill about 90 percent. Losses to disease were always low in these studies, although C. F. Stahl (personal communication) observed a severe epizootic in 1943 when hornworm numbers were very high. Two tachinid parasites, *Zygosturmia protoparcis* (Tns.) and *Winthemia* sp., are responsible for a very small average loss, but occasionally take as high as 8 percent of the population (Lawson, unpublished).

It is apparent that a very few enemies account for most of the losses in hornworm populations. The reason they are able to do this is easier to understand if the relations between enemies are examined more closely. In this discussion disease and one species of tachinid will be ignored because very little is known about them, and these enemies are insignificant.

Except for the two species of *Polistes*, no two enemies occupy precisely the same niche in the hornworm life history. Stilt bugs attack eggs; wasps attack larvae. Tachinids oviposit on very large hornworms in the last instar and emerge from the pupae. *A. congregatus* oviposits in the first three instars and emerges from the fourth and fifth.

The niche occupied is determined by the adaptations of the enemy. Stilt bugs take hornworm eggs and possibly newly hatched larvae, but are too small to attack larger larvae. Wasps are repelled by the violent resistance of large fifth instars, but the tachinid flies can dart in swiftly to oviposit on even the largest hornworms. The two wasp predators are closely related species, have similar abilities, and occupy nearly the same niche.

Some of the niches of dissimilar species overlap. Thus, *Apanteles* oviposits and develops in the same instars that are attacked by wasps. Some of the large hornworms attacked by tachinids are already parasitized by the braconid. When overlapping occurs, there may be direct and severe competition that results in the survival of one enemy at the expense of the other. Thus, the wasps apparently make no distinction between parasitized and healthy larvae, and destroy a large proportion of the parasite population along with the host. In 1953 and 1954 hornworms collected in the field after parasite oviposition, but reared in the laboratory, were compared with those remaining in the field. At three stations the indicated losses of parasitized larvae to predators were 49, 62, and 86 percent. Rabb (1953) found *Apanteles* larvae in pieces of hornworms brought to the nest by *Polistes*. Severe competition may also occur between *Apanteles* and tachinids. In 1952, among several lots of large hornworms dissected in the laboratory, 28 had tachinid eggs attached to the head and thorax. Out of this number 24 were also parasitized by *Apanteles*. When this occurs the braconid emerges first and the tachinids perish.

As a result of competition the food supply of some species is greatly restricted and their populations are reduced. In the species with overlapping niches there is a direct reduction equivalent to predation, but even where they are separate the results of competition may be pronounced. In 49 populations of hornworms the average survival to the fifth instar was 10 percent of the number of eggs laid. Thus, the populations available to the tachinids were greatly reduced by the other enemies. Sometimes the number available is much smaller. For example, in the second highest population on record 77 eggs were observed on 25 plants. Of these, 51 percent were destroyed by egg predators, 47 percent by larval predators, 1 percent was found dead, and 1 percent was parasitized by *Apanteles*. None were left for the tachinids and none survived.

Competition and Dominance

Competition establishes a sort of natural hierarchy among the enemies of the hornworm. The highest position is occupied by the stilt bug, which takes what it needs without interference from other enemies. The wasps are next and consume a large share of the remainder and sometimes nearly all of it. If any is left, *Apanteles* gets a small share, and if some still remains, the tachinids take a portion. The number of significant enemies is limited because the most successful competitors take most of the food supply.

The same principle also explains why the enemies of the green peach aphid are limited in number. Aphids are commonly attacked by coccinellids, which occasionally become numerous enough to reduce the aphid population (Kulash 1949). However, the diseases usually destroy the aphids before the predators can become really effective. Competition between the enemies of other insects is, of course, known to occur. Varley (1947) reports severe competition between the enemies of the knapweed gall fly. Davis (1944) found *Apanteles diatraeae* Mues. to be severely reduced by competition with *Trichogramma minutum* Riley.

In brief, when two dissimilar enemies attack

the same host, one will be able to deprive the other of the food supply unless it is itself limited by other factors. Thus, competition reduces the number of enemies that can attack a significant fraction of the host population, but when the take of the superior species is limited the surplus food can be utilized by the subordinate species and both can continue to exist together.

How far this process could go in permitting a multiplicity of enemies is by no means obvious. The number would tend to increase as the variability of the host life history and environment increases. For example, if a host lived in a wide range of climates, it is unlikely that the same enemy would be dominant throughout the range. Theoretically, there could be a dozen or more species, each of which took only a small fraction of the host population. Actually, it is more likely that the upper limit is five or six significant enemies.

Competition between the enemies of insects appears to be fundamentally the same as competition between plants. Piemeisel (1938), who studied secondary successions in the semi-arid Snake River Valley in Idaho, found that under certain conditions Russian-thistle (*Salsola pestifer* A. Nels.) was replaced by mustards (*Norta altissima* (L.) Britton or *Sophia parviflora* (Lam.)), and these in turn by downy chess (*Bromus tectorum* L.), primarily because the succeeding species had the advantage of prior germination and/or prior maturity and were thus able to use up the limited supply of water before the late comers could do so. When one species was limited by other factors, the next plant lower down in the succession took over the land. Thus, when downy chess was burned or heavily grazed by animals, Russian-thistle or mustards again became abundant.

A plant that by reason of superior competitive ability and the lack of limiting factors is able to monopolize the resources of its habitat is called a dominant by plant ecologists. Lesser plants are said to be subdominant; if two or more species share dominance, they are called codominants (Clements and Shelford 1939). The same terms seem to be applicable to the hornworm complex. The two species of *Polistes* that take the bulk of the hornworm population would be codominants, and the stilt bugs and parasites would be subdominant.

Practical Significance of Dominance

The dominance of the two species of *Polistes* in the hornworm complex has more than theoretical significance. About 80 percent of the damage to tobacco caused by hornworms is due to feeding by fifth instars. The amount of predation on the first four instars usually determines whether or not a particular population will produce an outbreak. Of 49 populations on record, nine produced economic outbreaks. Six of these outbreaks followed low initial populations when losses to predators of larvae were also low, and three followed high initial populations when predation was below normal. There were four high populations which failed to produce outbreaks. Three of them were reduced by above-normal predation and one by high predation and disease (Lawson and Rabb, unpublished). These figures are not based on the percentage kill, but on effective kill; that is, when enemies occur in sequence, the effect of any one of them on the survival of the host is determined not by the total kill but by the proportion of the surviving population that is destroyed (Bodenheimer 1938). For example, if stilt bugs killed 50 percent of the eggs, wasps took 50 percent of the larvae, and parasites 50 percent of what was left, all three would have an equal effect on the final population.

The role played by the dominant predators has important implications for applied control. For example, there is another species of *Apanteles* in South America that might be introduced, but the project is not promising because the introduced species would be in competition with the wasps and subject to the same limitations as the native parasites. It may be possible to use the dominant predators in biological control. Two years' data indicate that most hornworm outbreaks can be prevented by providing nesting boxes for wasps close to the tobacco fields.

The wasps must also be taken into consideration in insecticide recommendations. Any material that destroys these predators will almost certainly increase hornworm survival in the next brood, and populations that are normally of little consequence may produce outbreaks. It has been demonstrated that hornworms can be controlled with one-fifth the recommended dosage of insecticide, if it is applied in a certain way and at the proper time to take the maximum advantage of the predator kill (Lawson *et al.* unpublished). It is apparent that a knowledge of how the natural-enemy complex functions has been of considerable value in designing control measures for the hornworms on tobacco.

The importance of the dominant enemies in the control of hornworms should not be allowed to obscure the fact that other factors may be equally important in the whole complex.

The control of populations is the function of the ecosystem, and a knowledge of all the principal

elements of the system, including the pest itself—its resources, its enemies, the weather, and their interactions—is essential to an understanding of population phenomena. The task of acquiring the necessary data on a particular pest will require considerable time and effort, but it certainly is not as difficult as most investigators imagine it will be. A working knowledge of the factors controlling most pests can probably be acquired in a reasonable time provided the investigator approaches the problem with an open mind.

Summary

Natural control of insect populations has been attributed to particular factors or types of factors, such as weather, natural enemies, or density-dependent variables. Recently some authors have suggested that the whole ecosystem is ultimately responsible for control. An examination of the population dynamics of the green peach aphid (*Myzus persicae* (Sulz.)) in North Carolina indicates that the ecosystem concept is a more realistic hypothesis than previous ideas. Every major change in the abundance of this species is the result of an interaction between weather and host plants or enemies, or both, and most changes ultimately involve a large number of other organisms. However, most of these factors are minor, and only temperature, rainfall, four hosts, and two enemies have significant effects.

The number of significant hosts of the aphid is limited because some are planted and others suppressed by man. Possible reasons for the limited number of enemies are indicated by an analysis of the natural enemy complex of the hornworms on tobacco (*Protoparce sexta* (Johan.) and *P. quinquemaculata* (Haw.)). Each of these enemies occupies a different niche in the life history of the host, but the niches may overlap. When this occurs one enemy may destroy another, but even when there is no overlap the food supply of some species is severely limited by the amount consumed by preceding ones. A few enemies consume nearly all the food supply. The most successful competitors are considered to be ecological dominants in the natural-enemy complex. An understanding of how these dominants affect hornworm outbreaks has proved very useful in designing practical control measures.

Although ecosystems are very complex, a working knowledge of how a particular species is controlled can be obtained in a reasonable time by identifying the most significant elements.

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THE SOIL ECOSYSTEM AND RADIOACTIVE WASTE DISPOSAL TO THE GROUND[1]

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INTRODUCTION

The advent of a full-scale atomic power industry presents an undefined problem of environmental pollution by radioactive wastes. This problem was emphasized at the recent Geneva Conference on the Peaceful Uses of Atomic Energy by workers from various atomic energy projects in this country and abroad. Odum (1956) has reviewed these papers and summarized their ecological implications.

The estimates of amounts of hazardous radioactive wastes are increasing as new power reactors are designed. At least four large private nuclear power stations are currently under construction or in the late stages of design. These will be located in the vicinities of Shippingsport, Pennsylvania; New York City; Detroit; and Chicago. In addition, a number of research reactors, other prototype power reactors, and military reactors are in various stages of development. Therefore, by 1965 there will be a considerable increase of fission products. A typical estimate is given in a recent report by Zeitlin, Arnold, and Ullman (1956), who have computed the amounts of hazardous radionuclides, particularly strontium^{90} and cesium^{137}, that will result from reactor operations after 2000 A.D. Actually, as has been so cogently pointed out in the recent joint study (1956) by the National Academy of Sciences and the National Research Council, contamination by reactor wastes is already present. We are faced with the possibility of increasing environmental contamination over the next twenty years. Therefore, it is imperative that basic ecologic research related to this problem be started at once. The situation as it exists today is one of limited contamination of a few areas; namely, at AEC installations such as the Oak Ridge National Laboratory. Those of us acquainted with the disposal of radioactive wastes to the environment are becoming more aware of the complexities introduced by the release of these materials.

It is my intention to examine the extent of our ignorance of the soil ecosystem and of soil contamination by radioactive materials. Three topics will be treated: (1) the soil ecosystem will be reviewed briefly, (2) some aspects of current research pertaining to soil disposal of fission products will be reviewed, and (3) some of the results of the research started at Oak Ridge National Laboratory on a limited aspect of the problem will be presented.

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SOIL ECOSYSTEM

The term "soil ecosystem" in this paper is used as originally proposed by Tansley (1935) and more recently extended and somewhat modified by Evans (1956). Thus, it is considered as the combination of the organism-population complex with the complex of physical factors that make up the environment, plus the organic and inorganic constituents that are basic sources of food materials and energy. As Evans rightly points out, this term logically can be expanded to include the whole biosphere, or it can be reduced to a particular level with a much more restricted organization. It is in this latter sense that the term "soil ecosystem" is used here.

Broadly speaking, a soil ecosystem can be said to be composed of three main constituents: a solid phase, a liquid phase, and gaseous phase. These three phases may be divided into five groups:

1. Mineral particles, including the various inorganic compounds.
2. Plant and animal residues, which range from the freshly fallen leaves and the undecomposed bodies of insects to materials that are so thoroughly decomposed that the original structure no longer can be recognized.

[1] Presented at the Symposium on Radio-Ecology at the meeting of the American Institute of Biological Sciences, University of Connecticut, Storrs, Connecticut, August 27-30, 1956.

[2] Operated for the U. S. Atomic Energy Commission by Union Carbide Nuclear Company.

3. Living systems, including the soil fauna, which ranges from protozoa to rodents; the soil flora, consisting of the algae, fungi, actinomycetes, and bacteria; and the living roots of higher plants.
4. Water both free and bound, the free water containing in solution varying concentrations of inorganic salts and certain organic compounds.
5. Gases which are mainly nitrogen, oxygen, and carbon dioxide.

Critical reviews and discussions of various aspects of soil ecology have been given by Taylor (1935), Waksman (1936), Jacot (1936, 1940), King (1939), Fenton (1947), Kühnelt (1950), Birch and Clark (1953), and Murphy (1953) among others.

Since our primary concern is the soil fauna and its function in the life of the soil, the most suitable classification for this purpose is one describing the food habits of the individuals insofar as they influence the chemical and physical properties of the medium. According to Jacot (1940) the soil fauna might be broadly classified into three categories:

1. Reducers of litter and organic material.
2. Mixers of organic residues and mineral soil.
3. Channelers of the soil.

Birch and Clark (1953) have presented a more elaborate and detailed classification, but its essential features are the same.

As pointed up by a symposium sponsored by the American Society of Limnology and Ooceanography and the Ecological Society of America (Frey 1956), significant advances in the study of productivity and energetics of fresh water ecosystems have been made during the past 15 years. Birch and Clark have made the very apt suggestion that the flow of energy should be studied in *terrestrial* communities. As yet, few attempts have been made, but the presence of the large animal populations present in the litter and F layers and their apparently saprophagous and fungal feeding habits suggest that an investigation should be made of their roles as a link in the biochemical chain in which organic material is broken down and its constituents released for reutilization. The inhabitants of the plant litter and soil lend themselves to such an investigation, albeit the complete study of the flow of energy through the organisms in leaf litter would be an immense task. The use of radionuclides for tagging various energy levels and tracing them may prove to be of great value.

Current Research on Radionuclides in the Soil

With this general picture of the soil ecosystem, we can turn to a discussion of the fission products and a review of some pertinent research. It should be emphasized that the ultimate disposal method for low-and intermediate-level wastes[3] has not been developed. These wastes will be present in relatively large volumes, thus it may be impractical to pretreat them to remove valuable radioisotopes as has been proposed for high-level wastes.[4] If such is the case, means must be found to dispose of them safely and economically. One method of doing this is to use the huge volumes of soil presently available as gigantic ion exchange columns. At present this concept envisions releasing sufficient amounts of wastes until the ion exchange capacity of soil is saturated up to an as yet undetermined threshold level beyond which there would be danger of contamination of the ground water with resultant damage to the natural biota. Since discharge of fission products to the soil is a recent development, ecological research is, for all practical purposes, just getting under way. The fission products shown in Table I are among the important ones from the viewpoint of both waste disposal and fallout. With the exception of iodine^{131} these isotopes comprise the elements that will contribute one percent or more of the total activity in atomic wastes which have aged for a period of one year. A number of factors are used to evaluate the hazards of these radionuclides. Among these factors are: quantity of the nuclide, body retention, critical organ retention, biological half life, mode of entrance into the body, radioactive half life, and energy and type of radiation. For a complete discussion of these the interested reader should consult Handbook 52, National Bureau of Standards, entitled "Maximum Permissible Amounts of Radioisotopes in the Human Body and Maximum Permissible Concentration in Air and Water."

Based on these considerations strontium^{90} is one

[3] Low-level wastes—usually these are large volume wastes such as drainage from laboratory areas and decontamination operations or water used in basins to shield operators during work on radioactive materials. The usual range of activity is from trace contamination up to 10^{-3} μc/ml. Intermediate-level wastes—these wastes come from various chemical processes or from relatively large experimental projects. They may contain as much as 2.7 μc/m (1/10 curie of radio-activity per gallon) (Morton and Struxness, 1956).

[4] High-level wastes—usually these contain large amounts of dissolved chemicals, and may be highly acid or alkaline. They range from 1/10 to 500 curies per gallon, and it is probable that some power reactor process wastes will be of even higher activity levels (Morton and Struxness, 1956).

TABLE I. Significant Fission Products. With the exception of iodine^{131} these isotopes comprise the elements which will contribute one percent or more of the total activity in atomic wastes aged for one year. Based in part on Hunter and Ballou (1951).

Isotope	*Half life*
Strontium^{90}	25 yr
Yttrium^{90}	64 hr
Strontium^{89}	54 days
Yttrium^{91}	57 days
Zirconium^{95}	65 days
Niobium^{95}	35 days
Ruthenium^{106}	1.0 yr
Rhodium^{106}	30 sec
Cesium^{137}	33 yr
Cerium^{144}	290 days
Praseodymium^{144}	17 min
Promethium^{147}	2.26 yr
Iodine^{131}	8.04 days

of the more hazardous elements. It is readily absorbed by the gastrointestinal tract and subsequently deposited in the skeletal structure where it can irradiate hemopoietic tissues. Because of the chemical similarity of strontium to calcium, the fate of strontium when released into the soil can be predicted to a certain extent.

Some of the other long-lived nuclides (for example, cesium^{137}, cerium^{144}, -praseodymium^{144}, and ruthenium^{106} -rhodium^{106}) likewise may be of significant hazard when their indirect environmental relationships are considered, rather than their direct effects on man. Ruthenium-rhodium can be used as an illustration. It exists in a number of chemical states both as an anion and as a cation, moves rapidly through soil, and its biological affinities are poorly understood.

In addition to the radiation hazard *per se* there will be quantities of elements produced which are now present only in trace concentrations in most soils. It remains to be seen to what extent the addition of these elements to soil ecosystems will become a biogeochemical problem.

One of the pioneer investigations of the possible contamination of the food supply by fission products was that of Jacobson and Overstreet (1948). They tested the uptake of the radionuclides of yttrium, cerium, zirconium-niobium, tellurium, strontium, and plutonium by barley. Of these, strontium was most readily translocated. Relatively large concentrations of fission products in soil were used, and these investigators concluded that a concentration of 0.1 μc per gram of soil was sufficient to produce injury to the barley plants over the three-month test period.

Neel *et al.* (1953) studied the relative uptakes of Sr^{90}, Cs^{137}, Ru^{106}, Ce^{144}, and Y^{91} from several soils by barley, carrot, lettuce, bean, and radish plants. They reported that the uptake of Sr^{90} by all plants exceeded that of Cs ^{137} and of Ru^{106} by at least one order of magnitude. Uptake of Ce^{144} and Y^{91} was negligible. Considerable variation in uptake among the five species was found, but in all cases the concentration was greatest in the leaves. In another investigation, using the Nebauer techniques with barley plants, Nishita, Kowalewsky, and Larson (1954) obtained essentially the same results with respect to the order of uptake of the fission products. The concentration of the isotope in barley seedlings was only a small fraction of the total concentration in the soil to which their roots were exposed. Furthermore, uptake varied with soil type. Larson *et al.* (1953) investigated uptake by radishes and Ladino clover from soil contaminated by a subsurface detonation of a nuclear device. The predominant isotope taken up by the plants in this study was Sr^{89}. Under the particular conditions of subsurface detonation they reported that the availability of the fission products appeared to be a function of their solubility. The insoluble particles resulting from the blast do not migrate through the soil and, therefore, do not come in contact with actively absorbing roots.

In a recent report Rediske, Cline, and Selders (1955) have reviewed the results of their investigations during the past few years on the absorption of fission products. Of particular interest is the statement, based on preliminary results, that "the effect on the concentration factor contributed by species differences amounts to about one order of magnitude or less." While this may hold for agricultural crop species, its applicability to native vegetation would warrant further investigation, especially since the work of Bowen and Dymond (1955) on the uptake of strontium and barium by various native British plant species presents evidence of species differences in concentration greater even than one order of magnitude. Bowen and Dymond go so far as to suggest the possibility of certain species serving as strontium indicators. Less equivocal is the corroborative statement by Rediske, Cline, and Selders (1955) that the leaves are the organs of greatest deposition of radionuclides.

Fission products have been used also in studies of the mechanism of ion uptake by roots. Vlamis and Pearson (1950) used radioactive zirconium and niobium to test some theories of root absorption. They found that the well known Co_2 soil solution theory did not apply insofar as these isotopes were concerned. They theorized that the only possible mechanisms to explain their results are direct ion transfer, or the excretion of organic acids by roots (solution theory), or the action of microorganisms which would act as some kind of chelating agent.

So far, reference has been made to studies involving the living roots of plants. Little research has been done with the other components of the soil ecosystem. An encouraging start in this direction has been made by Nishita, Kowalewsky, and Larson (1954) who studied the influence of soil organic matter on the uptake of Sr^{90} by barley and tomato plants. They reported that increase of organic matter with subsequent increase of the microbial population resulted in a decrease in uptake of strontium. This is attributed to the preferential selection of the nuclide by microorganisms. In another direction, Curtis and Dix (1956) have studied the distribution of alpha-emitting radioisotopes in the soil and litter of various forest communities. They report that conifer forests have higher concentrations of alpha-emitting radioisotopes than hardwood forests.

Ecological Studies at Oak Ridge National Laboratory

Because the Oak Ridge National Laboratory was and still is releasing intermediate- and low-level wastes into the soil, an ecological program was started, and the emphasis of the program is directed in part toward soil organisms. Instead of starting a field survey, of which there were several under way at other AEC installations, it seemed feasible to establish a project with the experimental emphasis initially on laboratory studies of the effects of ionizing radiations on various soil organisms. As a foundation of data and technology is developed, field experimental studies are started.

Previous investigations Park, Auerbach, and Corley 1950; and Park and Auerbach (1954) had demonstrated that large concentrations of soil organisms, particularly arthropods, are resident in the decomposing organic complex found within hollow tree cavities. This habitat offered possibilities for controlled field experimentation since it is a relatively isolated micro-environment having the same faunal groups that are typical of forest litter. Cobalt or cesium pellets could be mounted on the tree trunk to deliver a known and constant dose rate to the contents for any desired period of time. For these reasons, and also because it was believed that a study of this habitat niche would facilitate a more general attack on the entire problem, some laboratory experiments testing the effects of gamma radiation on tree-hole arthropods were initiated.

Of particular interest is a series of experiments on some of the arthropods from a single tree hole. The substrate from a tree-hole in a beech (*F. grandiflora* Ehrh.) (Figure 1), located on the southeast side of a bluff above the Clinch River in the Roane County portion of the AEC restricted area, was brought into the laboratory and divided into a number of weighed samples. Some of these samples were analyzed immediately for their contained arthropods by using Berlese-type funnels. Fourteen 50-gram samples averaged 1500 arthropods each. Extrapolation of these figures, based on the total amount of substrate, yielded a total tree-hole population of arthropods in excess of 250,000 at the time of collection. The taxonomic analyses of this large number of arthropods resulted in considerable data, including a large check list. Most of these data will be treated in a subsequent article; a summary will suffice for the present purposes (Table II). The taxonomic organization is similar to that of forest and grassland soils. The most abundant arthropod groups in the soil habitats—the Acarina and Collembola—are also the most abundant in the tree-hole habitat both in number of species and in numbers of individuals. The Coleoptera and Diptera are the other two abundant orders represented in the tree-hole. In soils Coleoptera and Diptera may or may not be abundant, depending on site, season, and other factors.

Fig. 1. Exterior of beech tree hole. The cavity began 2½ ft below ground surface and extended 6 ft up into the trunk. The substrate used in the experiments filled the bottom 18 in. of the hole.

TABLE II. Summary of Numbers of Arthropod Species Found in a Beech (*F. grandifolia* Ehrh.) Tree Hole in June 1955

Crustacea	
Isopoda	1
Copepoda	1
Arachnida	
Pseudoscorpionida	1
Araneae	1
Acarina	47
Paurapoda	1
Symphyla	1
Diplopoda	8
Chilopoda	1
Insecta	
Protura	2
Entotrophia	1
Collembola	31
Orthoptera	1
Corrodentia	1
Thysanoptera	1
Hemiptera	1
Homoptera	1
Lepidoptera	2
Diptera	16
Coleoptera	27
Hymenoptera	9
Total	155

The objective of this series of experiments was to irradiate weighed samples of tree-hole substrate with their arthropod populations. This material was maintained in the laboratory for an extended period of time, samples were removed at regular intervals, the surviving arthropods were extracted, and their numbers were compared with the numbers of the controls likewise maintained in the laboratory. Part of the survival data obtained for Acarina and Collembola are illustrative of some radiation ecology problems.

Although six collembolan families were present in the tree hole, two families (the Isotomidae and Poduridae) comprised the majority of species and individuals; twenty species of the total thirty-one being in these two families. The dose-survival data for Collembola are shown in Figure 2. The three sets of curves represent the percentage survival of individuals for each of the three sampling periods after irradiation. In each case the percentage survival is in terms of controls maintained for that particular period of time. The vertical line through each point is the standard error. Isotomid species can be discriminated under dissecting microscope magnifications whereas podurid species cannot be identified with certainty. For this reason the dose-survival curve was plotted for the total Collembola, for one species of isotomid (*Folsomia clongata* Macg.), and for the total Poduridae.

At 30 days postirradiation the species populations are closely grouped. Using the total Collembola curve as indicative of the general pattern, a dose effect does not appear to take place below 3,000 r. Above this dose the curve shows a pronounced linearity until 25,000 r, whereupon the "tailing" which is characteristic of data involving large numbers of individuals begins with a few individuals surviving the highest dose given. *Folsomia clongata* shows a marked deviation from the total curve at the 8,000-r dose. Otherwise, *F. clongata* and the podurid curve parallel the total closely. An approximation of the 50 percent mortality dose based on these curves is 20,000 r.

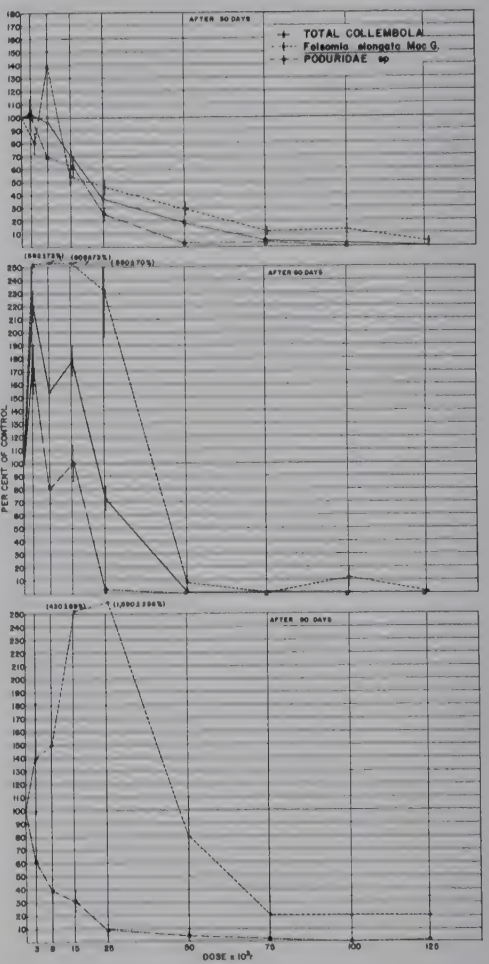

FIG. 2. Survival of Collembola 30, 60, and 90 days after exposure to gamma radiation. Number of individuals expressed as percent of controls *vs* dose.

At 60 days postirradiation there is a marked change in the pattern of the curves. At 3,000 r all the Collembola have increased beyond the con-

trols. Above this dose the podurids start to drop below the controls and, with one exception (15,000 r), decrease abruptly to 25,000 r; beyond this dose the podurids are eliminated. In contrast *F. elongata* increased considerably above the controls at doses up to and including 25,000 r. Above this dose it decreased abruptly to a few individuals.

At 90 days postirradiation the pattern is much the same. Since the two groups shown comprise the bulk of the individuals surviving at this time, the curve for the total Collembola was not drawn. The podurid curve shifted more to the left, giving an indication of the group being eliminated completely in an additional increment of time. *F. elongata* increased still more above control levels. These data tend to support the concept of differential radiosensitivity even between related species.

A problem posed by these results is the increase in numbers of individuals of the irradiated species populations above control levels. One might be tempted to postulate a stimulatory effect of radiation. In fact, if a search of radiobiological literature is made, scattered reports can be found which support such a hypothesis. The evidence is weak; for example, the work of Carlson, Harrington, and Gaulden (1953) shows that stimulatory effects of radiation are more apparent than real.

There is another possible explanation for the increase in numbers. In a recent study Sheals (1955) tested the effect of DDT on the soil fauna in selected field plots and found a significant increase in Collembola in his treated plots. In laboratory observations he found that the Collembola normally were preyed upon by five species of mesostigmatid mites. The mites, upon testing, proved to be sensitive to the DDT concentrations used whereas the Collembola were not.

The Collembola were sensitive to another insecticide, BHC, while the mites were not. By using these in a combination of field experiments Sheals obtained significant results which showed that the buildup of Collembola in DDT-treated plots was due to the elimination of the predator mites.

If we consider radioactivity as just another extraneous and hazardous factor added to the environment, which is capable of creating biological imbalance due to differential species sensitivity, then our Collembola results probably can be explained in terms of some combination of reduced predation, parasitism, or competition. Evidence of this was obtained in our tree-hole experiments, and is illustrated in Figure 3. The dose-survival data are plotted for two species of Acarina. One species (*Rhizoglyphus sp.*) is an herbivorous and saprophagous mite belonging to a family (Acaridae) noted for high reproductive capacity. The other species (Neoparasitidae) is a predator which can feed on *Rhizoglyphus*.

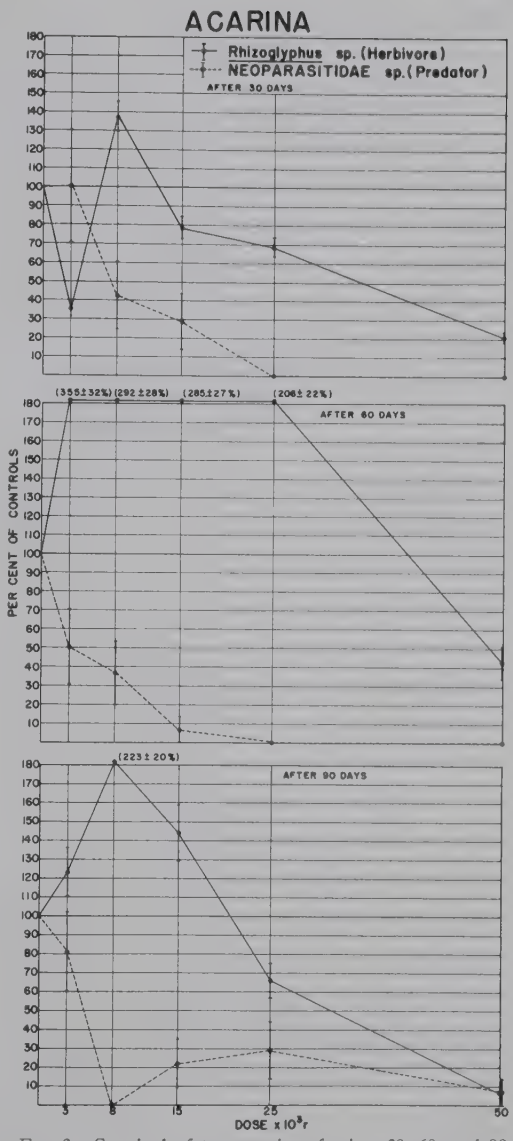

FIG. 3. Survival of two species of mites 30, 60, and 90 days after exposure to gamma radiation. Note increasing numbers of herbivorous (prey) with simultaneously decreasing numbers of predators.

At 30 days postirradiation the neoparasitids, at doses above 3,000 r, are reduced to zero numbers by 25,000 r. At the same time the herbivore *Rhizoglyphus* showed a tendency to increase in numbers beyond control levels. This is indicated by the high numbers at 8,000 r; with in-

crease in dose there was a gradual reduction. At 60 days postirradiation the predator curve has shifted to the left, with a 50 percent reduction in numbers occurring at the 3,000 r dose. Simultaneously *Rhizoglyphus* in the samples which received 3,000 r, 8,000 r, 15,000 r, and 25,000 r increased in numbers to more than twice the control samples. At 90 days much the same pattern exists, although there is evidence of some recovery of the predator at the higher doses (15,000 r and above). If it is assumed that the neoparasitidae is a predator of *Rhizoglyphus,* the curves imply that the increase in numbers of prey is related to the greater radiosensitivity of the predators. If the latter are adversely affected by the radiation, as the data indicate, the pressure exerted by them would be lessened, thereby allowing an increase in prey numbers.

Rohde (1956 a, b), in our laboratory, tested the above hypothesis by using a saprophagous mite species and its known predator, another mite species. When the eggs of the species were compared, using hatchability as a criterion of radiosensitivity, the hypothesis was not supported. However, when adults of these species were irradiated, and the subsequent hatchability of their eggs used as a criterion, the predator adults were found to be more sensitive. In both sets of experiments single doses of gamma radiation were used. This did not allow for changing of biological conditions through time. The time factor in eggs may be very important since radiosensitivity changes with aging (Bergonie and Tribondeau 1906). In Rohde's egg experiments time was measured in days whereas hourly measurements might have been more meaningful. A more valid ecological test of this hypothesis would be the chronic exposure of these species to sublethal doses of radiation, but equipment was not available.

In presenting these data the author is cognizant of the lack of completeness. The value of the data is that they are illustrative of some of the difficulties the radiation ecologist will face in his attempt to evaluate the effects of radioactivity and radioactive substances on the natural environment and its components.

In addition to laboratory studies on arthropod species populations, biogeochemical, animal, and biomass investigations are being made in a contaminated environment provided by the draining of the Laboratory's low-level radioactive waste impoundent area formerly known as White Oak Lake. Arthropod, mammal, and plant population studies in the radioactive waste areas, as well as investigations of the microbiota in our intermediate- and low-level waste streams and the nearby river drainage also are under way. Yet in terms of the over-all problem, and in comparison with the work being accomplished in other biological disciplines to which the word radio has been made a prefix, our efforts are very small.

If the future hazards of radionuclides to our soil ecosystems are to be evaluated, we must expand and study in greater detail the various forms of life resident therein. Already much has been gained from microbiological studies that could be applied to the problem of the ultimate fate of radioactive wastes released to the soil. It is known, for example, that bacteria can oxidize and complex a whole host of inorganic and organic materials. However, the quantitative links between that trophic level and higher levels and their applicability to the fission product problem remain to be clarified.

Insofar as the effects of ionizing radiation itself are concerned, data are being accumulated. There exists a virgin field of endeavor which is the study of the effects of constant, sublethal, known doses of radiation to organisms, populations, communities, and ecosystems, both in the laboratory and in the field.

Summary

1. The ecosystem concept is applied to soils. The soil ecosystem includes mineral particles, plant and animal residues, living systems, free and bound water and gases.

2. The possibility of using the ion exchange capacity of soil to retain large volumes of radioactive wastes is under investigation. Many ecological data are needed for the establishment of health and safety criteria.

3. Strontium appears to be the fission product most readily translocated by the plant species studied. Rate of uptake, as well as concentration in the different organs, depends on soil conditions. The leaves seem to be the organs of greatest deposition of radionuclides.

4. Weighed samples of tree-hole substrate containing dense and complex arthropod populations were exposed to various doses of gamma radiation from a cobalt^{60} source. After irradiation the samples were maintained in the laboratory. At 30-day intervals up to 90 days, a series of these samples was processed through Berlese funnels to obtain the surviving arthropods.

5. It appears from the data on Collembola and Acarina that related species can differ in their sensitivity to radiation. Evidence of predator-prey differential radiosensitivity was also obtained for two mite species.

6. If radioactivity is considered as another ex-

traneous and hazardous factor added to the environment, which is capable of creating biological imbalance due to differential species sensitivity, then the results obtained in these tree-hole experiments probably can be explained in terms of some combination of reduced predation, parasitism, or competition.

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BIOACCUMULATION OF RADIOISOTOPES THROUGH AQUATIC FOOD CHAINS[1,2]

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Introduction

With an increasing number of atomic energy installations and their associated problems of disposal of liquid wastes, we recognize that more and more aquatic environments are going to be exposed to at least low concentrations of radioactive materials. For the safety of human populations who may be drinking water which contains such radioactive materials, a set of maximum permissible concentrations has been recommended (International Commission on Radiological Protection, 1955). By themselves, however, such recommendations are inadequate to define completely the radiological hazard which may develop through aquatic food chains. Where biological systems are involved, the organisms may accumulate certain isotopes to many times the initial concentrations in the water. There are many radioisotopes, however, that apparently are not biologically concentrated.

This paper describes some of the mechanisms involved in the accumulation of radioisotopes by aquatic organisms, with special reference to food webs and metabolic rates, and presents some examples of how the concentration of radioisotopes in organisms can be used to measure relationships between different species.

The Accumulation of Radioactive Materials

In order to interpret the reasons for, or to predict the concentration of, radioactive substances in aquatic forms, the biologist must appreciate that several basic processes are involved. The most important are: (1) the mode of uptake, which includes adsorption to exposed areas, absorption into tissues, and assimilation of ingested material; (2) retention, which is a function of the biochemistry of the particular elements and components involved, the site of deposition, the turnover rate, and the radioactive half-life; and (3) the mode of elimination, which may involve ion exchange, diffusion, excretion, and defecation.

Mode of Uptake

The metabolism of the different radioelements and the relative importance of the different modes of uptake will fluctuate widely between different species, environments, and seasons. While this paper is principally concerned with assimilation through food chains, the processes of adsorption and absorption of radioactive substances directly from the water cannot be neglected. They are primary mechanisms by which inorganic materials are acquired by aquatic plants which are the food sources of the animals. The absorption of radioisotopes of strontium, barium-lanthanum and sodium by fresh-water fish has been demonstrated by Prosser *et al.* (1945). Absorption of radiocalcium has been demonstrated by Lovelace and Podoliak (1952) and by Rosenthal (1956). Chipman (1956) showed that cesium readily passed through excised pieces of tuna skin but that there was little absorption of strontium or ruthenium from sea water. Fish immersed in effluent from the Hanford reactors concentrated Na^{24} in the tissues about 130-fold. Direct absorption of other isotopes which are dominant in the effluent, including Cr^{51}, Cu^{64}, P^{32}, As^{76}, and rare earths, appeared to be inconsequential, however. In fish that live downriver from the Hanford reactors, sorption of radioactive materials directly from the effluents accounts for only about 1.5 percent of the total radioactivity. Consequently, sorption is of much less importance than ingestion in the uptake of radioactive materials by Columbia River fish.

Adsorption occurs almost instantaneously, as has been demonstrated with yttrium on cells of the marine alga *Carteria* by Rice (1956), while equilibrium by absorption is usually reached by algal cells (Whittaker, 1953) and by vascular aquatic plants (Hayes, *et al.*, 1952) within a few hours. Because of the rapid uptake of radioisotopes by these mechanisms, Columbia River plankton, composed almost entirely of diatoms, appears to reach equilibrium about one hour after floating into the zone containing effluent from the Hanford reactors (Foster and Davis, 1955).

Assimilation of ingested materials is the domi-

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nant means by which many radioactive materials become accumulated in animals since the bulk of their essential elements is obtained from their food. The contribution of food webs to the concentration of radioisotopes in aquatic animals was apparent from samples collected from the Columbia River soon after the first Hanford reactors began operation. Fish collected downriver from the reactors were approximately 100 times as radioactive as laboratory fish that were exposed to equivalent mixtures of the effluent, but fed uncontaminated food. Bottom animals, particularly herbivorous insect larvae, were found to be even more radioactive than the fish. The concentrations of radioactive materials in Columbia River organisms have never approached hazardous levels, however.

Differences Between Species

The relative concentrations of beta emitters in various Columbia River organisms are shown in Figure 1. There are several reasons for the differences which occur between these species.

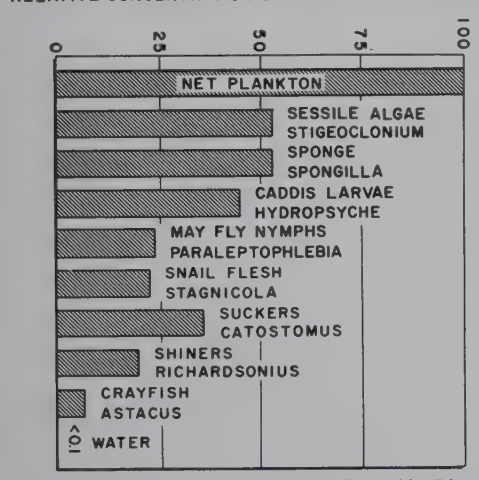

FIG. 1. Radioactivity in different Columbia River organisms.

(1) Several radioisotopes are involved and their relative proportions are different in the various organisms. A good indication of the proportions of the several isotopes can be obtained from curves like those in Figure 2 which show the characteristics of the radioactive decay of the isotope mixtures peculiar to each species. The positions of the curves in Figure 2 at zero time approximate the relative concentrations of radioisotopes in the water, small fish [*Richardsonius balteatus* (Richardson)], caddis larvae [*Hydropsyche cockerelli,* Banks], and plankton of the Columbia

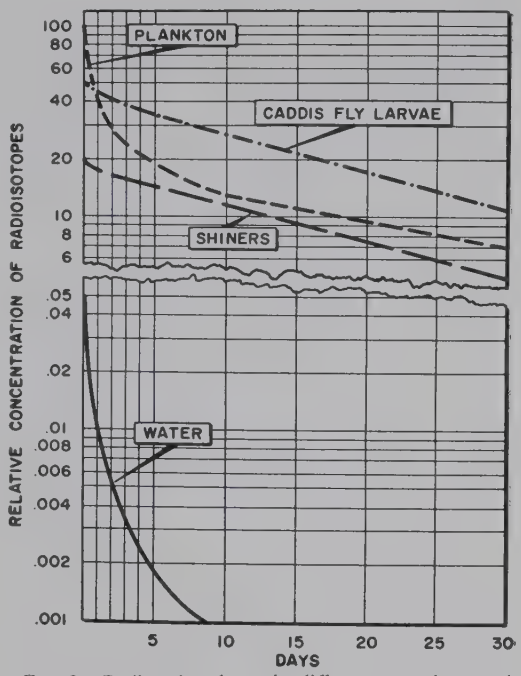

FIG. 2. Radioactive decay in different organisms and Columbia River water.

River during the late summer months. The predominance of short-lived isotopes in the water is shown by the steep slope of the bottom curve. Short-lived emitters also contribute most of the radioactivity in the plankton but these have virtually disappeared by the fifth day. The remaining activity in the plankton, which is only about 20 percent of that originally present, emanates from P^{32} and other isotopes with half-lives greater than two weeks. In the caddis larvae and fish, only about 5 percent of the initial radioactivity originates from short-lived emitters. After the first day the rate of decay is quite uniform and characteristic of P^{32} (half-life 14.3 days). The dominance of the P^{32} has been confirmed by radiochemical analysis.

The relative proportions of the several isotopes differ from one organism to another not only because of dissimilarities in the chemical composition and physiological demands of the different forms but also because of the different sorption characteristics which vary with morphology. Food chains are also important since they tend to "select for" isotopes of the essential elements, in this case P^{32}, and to "select against" nonessential elements. During the late summer months, the concentration of P^{32} in small fish of the Columbia River may be 165,000 time that of the water. On the other hand, As^{76} is barely detectable in the

fish although it is responsible for a substantial fraction of the radioactivity in the water.

The marked variation in the relative abundance of different isotopes which can occur at different trophic levels and even between similar species has recently been pointed out by Krumholz (1956). From data collected at White Oak Lake, which received a variety of radioactive wastes from the Oak Ridge National Laboratory, Krumholz states: "Although radiophosphorus was generally accumulated in much greater amounts than any other radioelement by the organisms that served as food for the fish, that element made up only a small portion of the total radiomaterials concentrated in the fish tissues; whereas radiostrontium, which was present in the food organisms in only relatively small quantities, was accumulated in high concentrations in the fish skeletons. Furthermore, although the contents of the bluegill stomachs contained more radioactivity, on the average, than those of the black crappies, the crappies accumulated considerably greater amounts of radiomaterials in the hard tissues than the bluegills did. The bluegills, on the other hand, accumulated more radiomaterials in the soft tissues than the black crappies. Both species concentrated radiostrontium in quantities 20,000 to 30,000 times as great as those in the water in which they lived."

(2) Variation in moisture content between different organisms is a second reason for the differences in concentration of radioisotopes shown in Figure 1. Chemical composition is also a factor since we are actually concerned with the quantity of a particular element in a unit mass of live tissue. The percentage of the live weight of the Columbia River plankton, caddis larvae, and minnows which is contributed by the inorganic ash is respectively 16, 2.2, and 3.0; and the concentration of phosphorus in the living organisms is about 150 ppm for plankton, 2,000 ppm for caddis larvae, and 6,000 ppm for minnows. Even greater differences may occur between the different tissues of an individual. Figure 3 shows how the concentration of radioactive materials varies between different tissues of whitefish in the Columbia River. Since virtually all of the activity is from P^{32}, this gives a good indication of the relative concentration of phosphate in the different tissues.

(3) A third reason for differences in concentrations of radioisotopes between different organisms is their relative position on the food pyramid. Although elements are exchanged continuously between the water and the organisms of a food web, there is a mean retention time for each element in each organism. Each trophic level thus serves as a kind of pool or reservoir in which essential

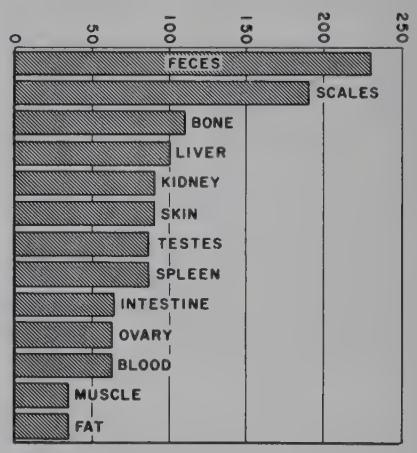

FIG. 3. Radioactivity in different tissues of Columbia River fish.

elements are retained for some mean length of time before they are passed on to the next level. The size of each pool will be governed by the total amount of an element held by the entire biotic mass making up the particular trophic level. A major fraction of most radioactive contaminants accumulated by aquatic life will be held by the plankton and benthic algae because of their relatively large total mass. Rigler (1956) found that over 95 percent of the P^{32} added to a lake was taken up by plankton (including bacteria) within 20 minutes. But retention time is not necessarily a function of the size of the pool. Indeed it is more apt to be inversely related since most elements will remain for a longer time in the larger organisms than in the small plant forms, although the small plants constitute the largest pool. Since, in the Columbia River, we are dealing with a flowing stream where isotopes are added at a more or less constant rate, much of the mineral exchange system can be considered as a once-through process rather than a cycle. Some radioactive decay will occur while the isotopes are retained in each trophic level. This decay, and thus the effective retention period, should be measurable by a progressive decline in specific activity—the concentration of an isotope per unit mass of the element. For example, under certain conditions midge larvae in the Columbia River may contain on the order of 4 μc P^{32}/g of P and the small fish which eat the midge larvae about 0.5 μc P^{32}/g of P. Since the half-life of P^{32} is two weeks, the phosphorus deposited in the fish must be, on the average, about six weeks "older" than that in the midge larvae. The relative "age" of the isotope

will differ between species and will change with the age, size, and growth rate of the individual and with the seasons. The decrease in specific activity will, of course, be more apparent for short-lived isotopes than for those with half-lives of several weeks or more.

The specific activity of the river biota should be appreciably lower than that of the water not merely because of the time required to incorporate the isotope into the organisms but also because of the "pools" of elements fixed in the biota and sediments. When a radioisotope is first introduced into a body of water it will be isotopically diluted with the stable form of the element which is dissolved in the water. Soon, it also will become isotopically diluted by exchange with the stable form of the element which has not been in solution. With a single addition of isotope into a "static" environment, the specific activity will eventually become uniform throughout the biota. Reservoirs of phosphates in the solids of lakes have been described by Hutchinson and Bowen (1950) and Hayes and co-workers (1952), who have studied phosphorus exchange with the use of P^{32}.

Rate of Accumulation by Aquatic Organisms

The nearly instantaneous uptake of isotopes by adsorption and the rapid uptake by absorption have been mentioned. When animals are chronically feeding on radioactive materials, the rate at which their concentration of the isotopes approaches equilibrium will be a function of the radioactive and biological half-lives of the particular isotope involved.

Figure 4 shows the rate at which caddis fly larvae (*Hydropsyche cockerelli*) accumulated radioactive materials (mostly P^{32}) when fed filamentous algae (mostly *Spirogyra*) that had been cultured in reactor effluent. If there was no biological turnover of phosphorus in the caddis larvae, the time required to reach some fraction of the equilibrium level would be a function of the radioactive decay constant and could be predicted from the equation:

$$\frac{Q_t}{Q_e} = 1 - e^{-\lambda t}$$

where Q_e is the amount of the isotope present at equilibrium, Q_t is the amount present at some time (t) before equilibrium is reached, and λ is the radioactive decay constant.

Since true equilibrium will only be reached after infinite time, we can consider practical equilibrium to occur when $Q_t = 0.9\ Q_e$, and solve the equation for t. For any isotope, t will be equal to the half-life multiplied by $\frac{-ln\,0.1}{.693}$. For P^{32} it is approximately 47 days.

The curve presented in Figure 4 shows a much shorter time which indicates that significant biological turnover is present. The equation is easily modified to take this into account:

$$\frac{Q_t}{Q_e} = 1 - e^{-\delta t}$$

where δ is the sum of λ and β, where β is the constant for biological half-life. At 0.9 of equilibrium,

$$t = \frac{-ln\,0.1}{\beta + \lambda}$$

From Figure 4, t is about 50 hours and

$$50 = \frac{2.302}{\frac{.693}{T_b} + \frac{.693}{343}}$$

(343 is the half-life of P^{32} in hours).

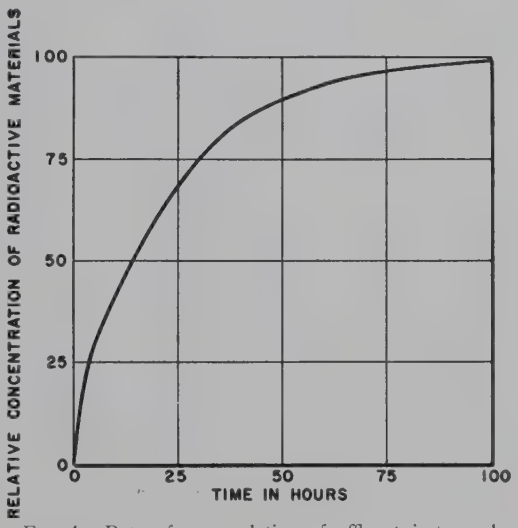

FIG. 4. Rate of accumulation of effluent isotopes by caddis fly larvae.

The biological half-life, T_b, is about 16 hours. Under such conditions the specific activity of the P^{32} will not diminish appreciably at this trophic level.

If laboratory tests can be carried out in conjunction with field observations, some interesting ecological relationships can be deduced. For example, we might measure the concentration of P^{32} in small minnows collected from a contaminated environment and find this to be 2×10^{-3} μc/gram. If the average size of the minnows was 5 grams, then each fish would have a body burden of about 10^{-2} μc of P^{32}. From a laboratory test, which duplicated field conditions as closely as possible,

we might find that 0.9 of Q_e was reached in 20 days. Then

$$\lambda = \frac{-\ln 0.1}{t} = \frac{2.302}{20} = 0.115$$

The same test might show that half of the ingested P^{32} was assimilated and deposited ($a = 0.5$). Assuming the concentration of P^{32} in the river fish to be in equilibrium with the environment and neglecting growth,

$$Q_e = \frac{aq}{\lambda}$$

where q is the quantity of P^{32} ingested per unit time—in this case each day. Then,

$$10^{-2}\,\mu c = \frac{0.5\,q}{0.115}$$

and $$q = 2.3 \times 10^{-3}\,\mu c/\text{day}.$$

In order to have reached the observed concentration of P^{32}, each minnow must have consumed about 2.3×10^{-3} μc of P^{32} each day. If, from stomach analyses, we have found that the fish feed predominantly on midge larvae and from field collections we have found that the midge larvae have a concentration of P^{32} of about 10^{-2} μc/g, then we can surmise that each minnow has been eating about 0.23 grams of the midge larvae each day.

Seasonal Variations

Since most aquatic animals are poikilothermic, their metabolic rates, and thus their feeding rates, change with variations in temperature and so with the seasons. For those aquatic forms that accumulate radioactive substances principally via ingestion, the concentration of radioisotopes fluctuates with metabolic rate. Figure 5 shows the seasonal fluctuations which occur in the radioactivity of plankton (diatoms) and minnows (*Richardsonius balteatus*) in the Columbia River. Fluctuations in plankton are quite similar to those in the water since the radioisotopes are acquired by direct absorption and adsorption (Foster and Davis, 1955). On the other hand, fluctuation in the radioactivity of the minnows is more closely related to the temperature. The 75-fold increase in concentration of radioisotopes in the fish between winter and late summer does not mean simply that the fish are eating 75 times as much food. The seasonal fluctuations result from the interaction of all of the factors mentioned above which influence the accumulation of radioactive materials. As the feeding rate increases for each organism, its intake of radioisotopes may be disproportionately large. The consumer is not only eating more grams of food, but each food organism has become more radioactive, and the effective time intervals between trophic levels have become less. Possibly the food habits of the species in question have also changed. A complete evaluation of the seasonal fluctuations in any one species would require an immense amount of work, not only on the food habits of the species but also on its physiology and on the radioactive contamination of its food organisms.

Not all seasonal variations are associated merely with temperature since deviations may occur where complex life cycles are involved. This occurs in immature insects which are less radioactive during quiescent periods than when the larvae or nymphs are feeding. It is also true of salmon that return to the Columbia River to spawn. The adult salmon virtually stop feeding when they enter fresh water, and consequently pick up very little radioactive material. Krumholz (1956) also observed definite seasonal changes in the accumulation of radiomaterials by fish of White Oak Lake. These corresponded to some extent with seasonal changes in temperature. He noted, however, that the accumulation of radioisotopes in black crappie and bluegills stopped at the first of August when the temperature reached about 80° F. He attributes the rapid loss of radioactive materials during August and September to a period of summer dormancy for these species.

Summary

Some radioactive materials introduced into aquatic environments may be accumulated by the organisms. The amount of accumulation will vary over many orders of magnitude depending upon the kinds of isotopes involved and many physical, chemical, and biological factors. Such concentration is of considerable importance in the control of radiological hazards and the aquatic biologist has definite responsibilities in this area.

The processes of adsorption and absorption are of major importance in the uptake of radioisotopes by plants but appear to be of less importance than the food chain in the uptake by aquatic animals. The concentration of radioactive substances will vary between species and tissues and will fluctuate according to food habits, life cycles, and seasonal changes.

Within the biotic mass, a major fraction of most radioactive contaminants will be held by the organisms which make up the primary trophic levels. In a flowing stream, the specific activity of a radioisotope will diminish along the food chain. Where the turnover rates of certain isotopes can be measured, inferences can be drawn on feeding habits.

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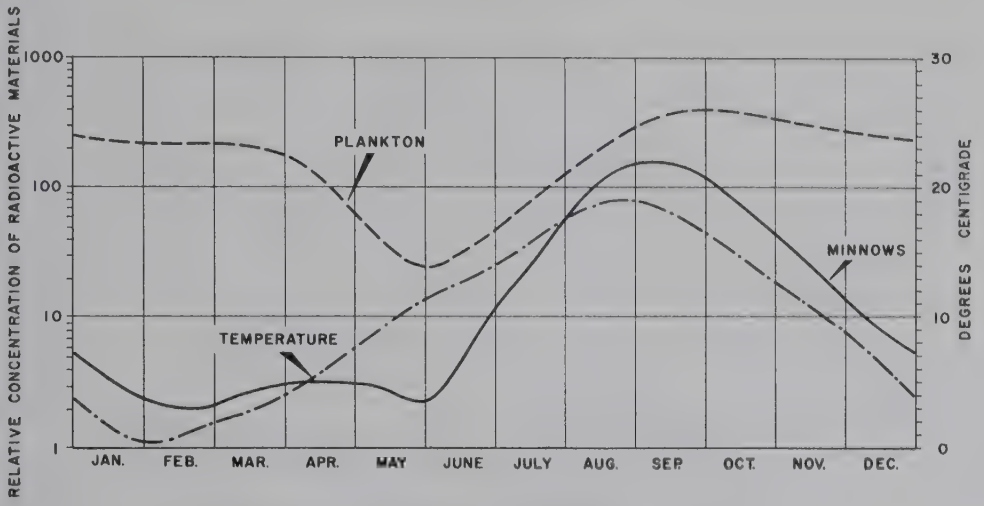

FIG. 5. Seasonal fluctuations in radioactivity of Columbia River organisms.

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NOTES AND COMMENT

NOTE ON THE DISTRIBUTION OF ROUGH FESCUE (*FESTUCA SCABRELLA* TORR.)

Recent literature (Coupland and Brayshaw 1953; Moss and Campbell 1947) has dealt with the fescue grassland, a biological entity which has been proposed as the seventh association of the North American grassland formation.

As shown in Figure 1, the distribution of the dominant species, rough fescue, follows a pattern which is common to a number of other arctic-alpine species. A brief discussion of how this type of distribution may have come about forms the basis of this note.

FIG. 1. Distribution of rough fescue (*Festuca scabrella* Torr.) in North America with area of best development enclosed in inked line. (From various sources.)

Cain (1944) has pointed out that the migration of plants, hence plant communities, is a matter of gradual increase in range across bands of similar environmental complex. He further points out that disjunction of a species range can occur in several ways, one of which is by the development of a different climax type in part of the original species range. We may assume, therefore, that the polytopic forms of *Festuca scabrella* Torr. are related and that the intervening spaces have been bridged in the past by a continuing series of populations although not necessarily at any one time.

In looking for suitable migratory paths by which a northwestern species could have reached the eastern part of the continent, it is apparent that the "prairie peninsula" immediately south of the Great Lakes constitutes the only satisfactory avenue of movement. Other routes must be rejected for edaphic or climatic reasons. Many indications that the area mentioned served as a migratory pathway for prairie plants exist there today, in the form of relict areas and fossil evidence (Curtis and Greene 1949; Flint 1947).

Consideration of Figure 1, in light of the preceding discussion, reveals several interesting points. First, in order to reach the proposed migratory path a southward movement of the species range of *Festuca scabrella* Torr. was necessary. This movement would have occurred during the last glaciation and, assuming that the fescue grassland retained its relative position along the edge of the boreal forest complex, probably reached a point three or four degrees of latitude south of its present position (Flint 1947). This would have put the members of the association in a position to migrate eastward. The eastward movement, at least as far as the Lake Erie region, probably occurred early in postglacial time and would have taken place during a warm dry interval. According to Sears (1932) such an interval did occur shortly after recession of the ice sheet began.

This position was probably maintained during the moist cool period which followed the initial warming. Four thousand to eight thousand years ago a further warm dry postglacial maximum occurred (Hansen 1949; Hansen 1952) and lasted for a long time. Under these conditions, a further shift of population would have occurred. Those prairie plants which had reached the Indiana-Ohio-Pennsylvania region probably moved north, under the influence of the climatic change, into Michigan and along the St. Lawrence River Valley. Many undoubtedly reached as far as the Gaspe peninsula while others, having succeeded in crossing the St. Lawrence River, probably moved northward along the Quebec coast, entered the various river valleys which flow in a north-south direction and probably got well into the interior highlands of Quebec.

With the onset of cooler, more moist climatic conditions, again shown by Hansen (1949, 1952) to have occurred and which he states were common to all North America, the northward movement of vegetation would have been stopped, finally reversed and the vegetative communities, as we know them, would have come into existence. Relict areas survived in favoured locations and have persisted to the present time.

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FORAGE CROPS SECTION,
EXPERIMENTAL FARM,
LETHBRIDGE, ALBERTA

USE OF HERBICIDES IN COMPETITION STUDIES OF RANGE VEGETATION

The herbaceous vegetation on annual range frequently emerges in such extreme density that many of the plants fail to achieve normal size and vigor. It would be of considerable interest to know the effect of reduced plant numbers on the growth of these species in an otherwise undisturbed environment.

Reduction of plant density by hand thinning is not feasible on sizeable areas and mechanical thinning disturbs the site. If plants are established in a prepared seedbed by seeding at various rates to regulate the competition, or by transplanting at prescribed spacings, an unnatural condition for range species results. The application of herbicide to range vegetation permits a reduction in plant numbers by removing a component of the existing flora. When this is done in the seedling stage, surviving species are permitted to develop with little disturbance on the native site.

Such herbicide treatment was studied on annual grassland in which an abundant cover of broad-leaved herbs grew with the grasses. The most prevalent of these forbs commenced rapid spring growth earlier than the grasses, making it possible to spray during cool weather at a time when more leaf area of the forbs was exposed than of the grass.

It was found that a non-selective foliage contact spray could be applied at this stage of growth to kill most of the forbs, yet leave the grasses uninjured or at most with a moderate leaf tip-burn. A dinitro compound (Sinox General) was employed as the herbicide without oil or detergent at the rate of two quarts per acre in 100 gallons of water. The differential kill obtained would seem attributable to the lack of retention of the spray material by the grass.

The spray was applied between late January and early March to replicated plots 100 square feet in size. When the predominant grasses had reached full development in the late spring, square-foot samples of the forage were cut at random at one-quarter-inch above the soil. These samples were air-dried, separated into grass and non-grass components, and weighed. Botanical composition analyses were run on a portion of the samples.

Results and Discussion

In February 1956 the first spray treatments were applied to plots of resident vegetation at both the Hopland Field Station of the University of California and the San Joaquin Experimental Range of the U. S. Forest Service. Test areas had been selected for a uniform cover which contained relatively abundant broad-leaved herbs along with the grass. Spraying and harvesting dates for Hopland were February 2 and May 16 respectively, while at the San Joaquin Range the dates were February 6 and May 17.

In both areas the vegetation after spraying consisted predominantly of grasses (Table I). During the spring these grasses appeared more vigorous and taller than those in untreated plots, and more of the plants attained an increased size. The weight of grass in treated plots was greater by approximately 100 percent than in untreated plots.

A more extensive trial was conducted at the San Joaquin Experimental Range in 1957. Three dates of spraying were employed; namely, January 25, February 15, and March 7, and the number of replications was increased to eight. Samples were clipped on May 1 except for the March 7 treatment which was clipped June 1. A month of abnormally dry weather followed the March treatment, this delayed growth making the later harvest date desirable.

Table I. Effect of herbicide on total herbaceous vegetation and on relative amounts of grasses and forbs

Area	Rainfall 1955-56 season	Treatment	Total dry weight†	Grass dry weight fraction
	Inches		*Gms.*	%
Hopland.....	50.9	None	63.8	35.3
		Sprayed	52.0	86.0
San Joaquin.	26.5	None	23.3	38.4
		Sprayed	22.8	85.1

†Average of four replications, 3 square feet per sample.

The most prevalent grass in the plots was soft chess (*Bromus mollis* L.) and the most prevalent forb was broadleaf filaree (*Erodium botrys* Bertol.). Other grasses of frequent occurrence were foxtail fescue (*Festuca megalura* Nutt.), slender wild oat (*Avena barbata* Brot.), ripgut (*Bromus rigidus* Roth.), and red brome (*Bromus rubens* L.). Among the additional forbs were popcorn flower (*Plagiobothrys nothofulvus* Gray) and native clovers with numerous other species occasionally represented. A more detailed account of the vegetation of this area is given by Talbot and Biswell (1942).

The weight of plant material produced with the percent of that weight contributed by grasses and by forbs is shown in Figure 1. Whereas grasses comprised 25 percent of the weight of the herbaceous cover in the controls, they accounted for 90 percent following herbicidal treatment. The total production declined in the February and March treatments, but the January spray treatment equalled that of the control. This greater growth of the January treatment may reflect the earlier removal of competing broad-leaved herbs, and the subsequent longer period favorable for development. The later maturing grasses were stimulated more than were the earlier.

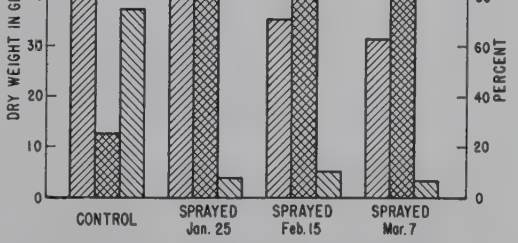

Fig. 1. Effect of herbicide applied at various dates on relative production of grasses and forbs.

As was observed the previous year, the grasses in sprayed plots were taller, and had more plants in the larger size classes. The increased weight of grass following a spray treatment appears attributable in part to the greater development of seedlings previously suppressed by competition with other species. Chippindale

(1932) has demonstrated that grass seedlings may persist for long periods under conditions rendered unfavorable for their growth by the competition of other plants, yet recover rapidly upon release from this competition.

The results of these trials suggest that herbicides may be useful in controlling the density of natural vegetation. Other formulations should be tried to determine their effectiveness in removing plants without exerting damage on the remaining vegetation. With increase in the number and selectivity of herbicides, it is conceivable that the competition afforded by a single species may one day be studied through herbicidal removal of that species from the herbaceous cover.

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SOME CHANGES IN THE SOIL ENVIRONMENT OF A GRAZED-PRAIRIE COMMUNITY IN CENTRAL MISSOURI

Introduction

In an earlier paper changes in species composition due to grazing of tallgrass prairie in Missouri were reported (Kucera, 1956). It was shown that severe deterioration of the native vegetation results from heavy use over a short period of time. The study area is a 160 acre tract of unbroken prairie located 17 miles east of Columbia, Missouri, in Callaway county, T48N, R10W, Sec. 12, SW 1/4. It is a relic example of physiographic subclimax prairie, extensive areas of which occurred formerly on the poorly-drained flat lands of east-central Missouri, and in other sections of the Prairie Peninsula. The soil, designated as Putnam silt loam, is of loessial origin and is characterized by strong profile development and slow permeability. The surface horizon is dark gray underlain by a lighter subsurface zone and a dense clay subsoil (Frieze, 1950). *Andropogon scoparious* and *A. Gerardi* are the principal components of plant cover. The floristic details of this tract are presented by Drew (1947). Beginning in 1941, the area was partitioned, a part of which was utilized as pasture, the remainder as hayland. This procedure continued for approximately the last 15 years, and thus has provided ample opportunity for evaluation of the grazing factor on native prairie vegetation. With such changes as have occurred in floristic composition according to the earlier study, the question arises whether or not moisture relationships and physical structure of the soil profile have been altered. Therefore, the present investigation attempts evaluation of any changes in moisture patterns and structural features viewed as concomitant results of the grazing factor.

Procedures

Field and laboratory studies were conducted during the 1957 season. The grazed and ungrazed sections of the prairie tract were sampled monthly for soil moisture from April to October inclusive. Soil samples were taken from duplicate borings at 1, 6, 15, 20, 36, and 60 inches. A characteristic feature of the profile, particularly on the flat ground, is a dense claypan. Care was taken to reduce the relief variable as much as possible by selecting comparably flat terrain in both grazed and ungrazed sections of the prairie. Variations in root concentrations, clay content, and organic matter caused vertical differences in soil moisture within the profile. Samples were oven-dried at 110° C. for 24 hours in making moisture calculations.

Core samples were obtained for the purpose of determining volume weight, or apparent specific gravity, and total porosity. A LaMotte tube sampler was used. One-inch cores were taken successively at 1, 2, 3, 4, 5, and 6 inch depths, and two-inch cores at the 7-8, 9-10, 14-15, and 19-20 inch depths. Twenty-five cores were sampled from each level within each of the grazed and ungrazed sections. The volume weight is represented by the oven-dried weight of undisturbed soil mass per unit core volume. Since weighings were expressed in grams, volume dimensions of the core were calculated in the metric system. Thus, volume weight (V. W.) = g./c.c. on a unit basis, and is a measure of structural conditions.

Total porosity values expressed as the percentage air space of the total core volume (soil plus air space) were calculated from the volume weights and a specific gravity of 2.65, as follows:

$$\text{Total porosity (\% of total volume)} = 1 - \frac{\text{V.W.} \times 100}{2.65}$$

In addition to total porosity, capillary porosity was determined. This value is a measure of air space occupied by water held under capillary tension, and is an approximation of the field capacity under natural conditions. Capillary capacity was determined in the laboratory using air-dried samples passing a one mm. mesh, and from which root fragments and other plant particles were removed. Approximately 200 grams of soil were packed uniformly in glass cylinders to which was added an amount of water sufficient to wet three-fourths of the column. After the wet zone had ceased downward movement, and incipient drying appeared on the surface, a 60—70 gram sample was taken for oven-drying.

Losses on ignition were determined in triplicate from successive one-inch layers of soil in the top six inches of the profile. The three samples were obtained from a composite of the 25 cores used in determining volume weights. Oven-dried samples were screened to eliminate root fragments and ashed at 400° C. Loss on ignition was calculated as per cent organic matter in the soil.

Results

The soil profile under ungrazed prairie showed consistently higher moisture values from the beginning of the growing season into summer, after which a reverse was measured. This reversed trend began first in the subsoil and occurred progressively higher in the profile with subsequent samplings. Percentage differences in moisture are presented in Table I. These differences are attributed to variations in floristic composition and to the corresponding differences in utilization between the two tracts. The ungrazed portion has an intact cover of

TABLE I. Field moisture differences in the soil profile expressed as more (+) or less (−) for ungrazed prairie compared to grazed, modified prairie

Soil Depth — In.	Per Cent Differences on Sampling Dates in 1957						
	4/11	5/11	6/24	7/21	8/25	9/21	10/9
1	+53.1	+22.6	+100.1	+33.3	+30.5	+ 7.6	+18.4
6	+ 4.9	− 2.6	+ 33.6	+21.4	+16.0	−16.5	−14.9
15	+14.3	+ 6.6	+ 6.9	+35.3	−15.2	− 8.3	+ 7.8
20 (claypan)	+23.8	+18.0	+ 2.7	+ 2.7	− 2.1	0.0	− 3.0
36	+30.0	+23.3	+ 7.2	− 7.1	0.0	−12.0	−20.0
60	+ 8.7	+33.3	− 4.2	0.0	− 0.1	− 8.3	− 9.1

vegetation consisting predominantly of perennial grasses. Modification of composition had occurred under grazing with transformation to weedy grasses and various broad-leaved species. Decreased values in the lower profile under ungrazed prairie suggest greater utilization due to more extensive root systems of the native species. Furthermore, the period of maximum growth in undisturbed prairie occurs later in the season at the time when the modified vegetation has passed its peak of activity (Kucera, 1956). Since all sampling sites were comparable in topography and drainage, the pronouncedly higher values in this ungrazed prairie in the early season are due possibly to several factors. One is the delayed development of the *Andropogon* prairie in comparison to transient vegetation produced under grazing. The other possibility is the greater litter accumulation and foliage cover in the prairie, which would facilitate the conservation of soil water through reduced evaporation. Furthermore, the wetter soil plus the insulative effects of the cover itself may retard soil warming sufficiently to cause at least partially the slower growth in heavy prairie compared to the more open, disturbed community.

While data in Table I show only differences between the two tracts, a comparison of field percentages and their relative magnitude is informative. In the case of the June 24 determination in the top inch when the ungrazed section shows approximately twice the amount of moisture, the field percentages were 42.6 and 21.4. These actually are diminishing values from preceding months and indicate that part of the disparity between the two areas is probably due to a carry-over of the absolute difference from the beginning of the season. In well-drained soils this factor would probably not be as important as in those with poor drainage. Another consideration is the magnitude of change in field moisture from one sampling period to another. In July, the ungrazed tract registered 33.3 per cent more field moisture than the grazed tract in the top inch. This might indicate that not as much water was lost through evaporation and transpiration. However, the decrease through the period from June to July was 53 per cent for the ungrazed prairie and 30 per cent for the grazed-prairie community. Assuming equal precipitation amounts for both sections, and taking into consideration the differences in volume weights for the surface inch, more water was probably removed in the ungrazed section even though a greater absolute amount existed at the end of this period.

Table II shows a comparison of certain profile characteristics in the two tracts. The structural deterioration associated with grazing effects is limited to a relatively shallow zone in the profile. Volume weights are higher under grazed vegetation in the top four inches with the sharpest difference in the surface inch. Below the fourth-

TABLE II. Comparison of volume weight and porosity values in profiles of adjacent prairie tracts: A, undisturbed tallgrass prairie; B, grazed-prairie community

Soil Depth — In.	Volume Wt. g/cc.		Porosity as Per Cent by Volume					
			Total		Capillary		Difference	
	A	B	A	B	A	B	A	B
1	0.87	1.01	67.2	61.9	28.1	25.7	39.1	36.2
2	1.07	1.17	59.6	55.7	23.8	22.4	35.8	33.3
3	1.16	1.30	55.8	51.0	18.7	18.3	37.1	33.0
4	1.26	1.33	52.4	49.5	18.2	17.4	34.2	32.1
5	1.27	1.27	52.0	52.0	19.3	19.8	32.7	32.2
6	1.31	1.30	50.5	51.0	17.5	18.1	33.0	32.9
7–8	1.32	1.32	50.0	50.0	17.5	17.5	32.5	32.5
9–10	1.31	1.33	50.5	49.5	18.0	17.0	32.5	31.5
15–16	1.42	1.37	46.4	48.2	17.2	18.5	29.2	29.7
20 (claypan)	1.35	1.37	49.0	48.3	32.0	31.6	17.0	16.7

inch zone no differences are apparent. Since total porosity is calculated from the volume weight, this relationship for the former also prevails. Differences in capillary porosity determined by other means are not as positive. The greatest decrease under grazing occurred in the top inch. Below this zone, a trend is not distinguished. The difference between total porosity and capillary values is interpreted as a measure of air space in the natural structure normally free of water. This value is indicative of the larger air spaces in the soil whose radii range in size from those readily drained by gravitational influences to those sufficiently small that movement of water by capillarity essentially ceases. Some decrease in this large pore component was shown under grazing with the greatest changes again in the upper profile. Such differences in volume weights and porosity values as are exhibited in the two tracts are attributed to a combination of deteriorating vegetational structure including root systems, and mechanical compaction from livestock.

Changes in organic matter are slight and are limited also to the upper profile. Decreases in organic matter occurred in the grazed prairie. These changes are not large; however, a trend is indicated. Values for successive one-inch increments of the upper six inch zone are shown in Table III. A gradient with respect to amount of organic matter within this zone occurs in both tracts.

TABLE III. Organic matter as loss on ignition for successive one-inch zones in the top six inches of profiles of adjacent prairie tracts: A, undisturbed tall-grass prairie; B, grazed-prairie community

Tract	Successive One-Inch Zones					
	1	2	3	4	5	6
A	11.93	8.47	6.80	6.19	5.53	5.05
B	9.91	8.11	6.15	5.56	5.60	5.29

As in the case of structural changes, the difference between the grazed and ungrazed types are most distinct in the top inch and diminish gradually with depth. Below four inches no changes in residual organic matter are observed. It is expected that with continued disturbance unfavorable reactions will be intensified both at the surface and in progressively deeper levels. At the present time, however, soil changes both in physical structure and organic matter content are restricted to a shallow zone

in the profile, and represent incipient stages of deterioration.

Summary

This study is an evaluation of changes in soil moisture patterns and certain profile features resulting from 15 years of grazing in original tallgrass prairie in central Missouri. Comparison of effects in the grazed-prairie community is made with an adjacent ungrazed section. The changes observed in the study may be summarized as follows:

(1) Soil moisture values were lower at the beginning of the season in the grazed tract with its modified plant community. As the season advanced, subsoil levels under undisturbed prairie became drier, suggesting increased utilization caused by more extensive root systems and greater foliage development. Lower values at the beginning of the season in the grazed prairie are attributed to the more open nature of the community, resulting in greater exposure to evaporation effects, and to the typically earlier seasonal growth of the vegetation.

(2) Physical changes under grazing were limited to the uppermost part of the profile. Volume weights increased and porosity values decreased, suggesting a change to a denser, less-aerated profile. Below four inches no differences between protected and grazed prairie were apparent.

(3) Decreases in organic matter were observed under grazing. These decreases were limited to the first four inches of the profile. Differences were not large but a trend was indicated. The greatest change occurred in the surface inch.

(4) At the present time, as a result of 15 years of disturbance by grazing, profile changes are restricted to a relatively shallow depth. The study indicates that soil changes are slow in comparison to floristic changes.

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THE MEANING OF THE WORD "TAIGA"

Of the many Russian words that have been adopted by ecologists, three of the most familiar are names of major vegetation types—*tundra, taiga* and *steppe*. The second of these, taiga, has usually been interpreted by ecologists to mean the circumpolar coniferous forest zone which bounds the tundra on the south (Allee, *et al.*, 1949: 585; Hesse, *et al.*, 1937: 439; Beaufort, 1951: 11; Moreau, 1955: 256). However, several recent authors have used the word in a quite different sense, to refer to the ecotone between tundra and coniferous forest. Thus, Leopold and Darling (1953: 553) refer to "forest border (taiga)," Polunin (1955: 307), to "*taiga* (that is, terrain of sparsely scattered trees)," and Dansereau (1957: 114), to "taiga, with widely spaced trees." Hustich (1949: 11, 52) uses the word in yet another sense, as a synonym of the circumpolar coniferous (boreal) forest except that he excludes the southern-most part—his "southern spruce region."

The original meaning of the Russian word is clear enough. Ushakov's Russian Dictionary (Vol. 4, 1940, pg. 635) gives the following definition: "wild, scarcely penetrable, mainly coniferous, forest, which stretches in a broad belt through northern Europe and Asia to the Okhotsk Sea." Alexin (1950: 232, and enclosed vegetation map of the USSR) says, "in general taiga in the west-siberian sense has three principal characteristics: strong shade, swampyness and absence of elements of the broad-leafed forest. However, taiga may be conceived more broadly, to include with it the northern coniferous forest of the European part of the USSR, lacking the broad-leafed element, and the larch forest of Eastern Siberia (larch taiga)." This meaning has been preserved by Russians publishing in the English language. Segal's Russian-English Dictionary (1942: 812) defines taiga as "dense marshy forest in Siberia." Sukachev (1928) calls the coniferous forests of northern Russia "taiga," as does Berg (1950: 23 ff) who treats the climate, relief, soils, vegetation and fauna of the zone extensively.

Russian ecologists (see Berg, *op. cit.*, 3 ff) apply the term *lyesotundra,* or "wooded tundra," to the ecotone of scattered trees between the northern border of the forest and the treeless tundra. Marr (1948) retains this term as "forest-tundra ecotone," Hustich (1949: 52) refers to it as the "Subarctic Region," and Rousseau (1952: 456) calls it the "zone hemiarctique," an "emulsion" of the tundra and taiga zones, but there is no reason to apply the term taiga to this ecotone. To restrict "tiaga" to the ecotone and not apply it to the northern coniferous forest itself seems most undesirable since, as Hare (1950: 624) points out, taiga is "applied by Russian ecologists to the entire formation and is so understood by geographers everywhere."

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A TECHNIQUE FOR STUDYING BEHAVIORAL RESPONSES OF SMALL MAMMALS TO TRAPS

The initial behavior responses of mammals to traps have long been chiefly a matter of inference. Studies in which attempts have been made to evaluate this factor in trapping success for the most part have not been very successful. Lack of information about initial trap responses raises many questions such as the following: Were any mammals present in the vicinity of the trap? Was the bait used attractive to mammals? Was the trap investigated by any mammals at close range? Could the trap have been entered but failed to trip due to mechanical failure of the trigger mechanism? Several statistical analyses have been made in an effort to answer questions of this sort and to determine the amount of bias such behavior responses might introduce into population estimates based on a trapped sample of a population (Geis, 1955; Tanaka, 1952, 1956; Young et al., 1952), but the initial responses of mammals to traps still remain largely a matter of conjecture.

This study was made in an attempt to reduce some of the speculation about this type of behavior in mammals and to present a technique which may prove useful in many types of population studies.

METHODS

Sheets of smoked kymograph paper (8 x about 16 inches) were placed beneath the traps which were set in deserted outbuildings in an irregular pattern, mostly near walls where it was assumed that foraging activities were more intense. The smoked paper was thumbtacked onto wooden frames for convenient transport in the field. Large Shermans (3 x 3 x 10 inches), Museum Specials, and a few ordinary breakback mouse and rat traps were used. Peanut butter was used for bait. Any approach of a small mammal to the trap was registered on the sooted paper. In some instances it was possible to detect from black paw marks on the trap door whether entry had been "contemplated." Traps were checked within 24 hours after setting and if tracks were present the following information was recorded on the sooted paper: Type of trap and trap orientation (entrance and rear of trap marked on paper); location of trap; species captured. Direction of approach to the trap was recorded in a field notebook. All sooted papers showing evidence of approaches to the trap were shellacked on the spot and thus preserved as a permanent record.

RESULTS AND DISCUSSION

In a preliminary experiment in which two large Sherman traps were set in a residence for several nights during March and April, 1956 no record of trap nights was kept but all approaches to traps were recorded. Only house mice were captured and all captured individuals were killed in order to eliminate behavior responses resulting from previous capture. However, it was not possible to determine whether certain mice which approached but did not initially enter the trap may not have entered the same trap at a later time or may have visited and entered the other trap during the same trapping night. During this preliminary period of trapping a high ratio of captures to approaches was obtained with a total of eight apparent approaches resulting in five captures.

In a later experiment carried out in February and March, 1957 several types of traps were used and mammals caught in live traps were ear-tagged and released. The data resulting from this experiment are presented in Table I.

TABLE I. Comparison of responses of small mammals to different types of traps

	Type of Trap				
	Sherman	Museum Special	Rat	Mouse	Totals
Nights of trapping	5	5	5	5	5
Trap nights	77	48	26	19	170
Number of approaches to traps	27	16	3	2	48
Per cent of traps approached	35.0	33.3	11.5	10.5	28.2
Number of captures	14	8	1	0	23
Number of recaptures	1	0	0	0	1
Per cent of traps making captures	18.1	16.6	3.8	0.0	13.5
Per cent of approaches resulting in captures	51.8	50.0	33.3	0.0	47.9

The data for Sherman and Museum Special traps offer the best comparison as capture data for rat and mouse traps were so few that no valid conclusions could be drawn concerning them. Sherman and Museum Special traps were about equally efficient as about 50 percent of the approaches resulted in captures. If it is assumed that the number of approaches should equal the number of captures then the observed results differ significantly from the expected ($\chi^2 = 10.2$; $P < .01$). This could be considered as an indication that population sizes based on actual catches might be considerably underestimated. With no knowledge of the actual population size there

is, of course, no way in which to determine how many approaches to traps that "trap-wary" individuals may have made without being caught or before being caught. Since only one marked individual was recaptured in five nights of trapping (at weekly intervals) there is some indication that subsequent behavior responses to traps of the marked individuals may have been altered by trap confinement.

If the percentage of traps approached is considered, our data also show that perhaps only about one-third of the traps were actually sampling the population. Since most of the traps were placed along walls and spaced about 6-10 feet apart, it seems more probable that the area under traps was supersaturated. Recording the approaches to traps in a given area at different spacings thus might provide a fairly simple method of evaluating the most efficient spacing or saturation of an area with traps.

With the exception of one wood rat all of the captures were house-mice and all but four of the approaches were by mice. Therefore, the following observations pertain primarily to house-mouse behavior. Including the preliminary experiment, 55 approaches to traps were recorded. The individual approaches were analyzed as follows: From all sides—18; front approach only—11; one side only—6; front, back and one side—4; front and one side—4; back approach only—3; back and one side—3; back and two sides—2; front and two sides—2; front and back—1; both sides—1. In 18 traps approached from all sides there were 14 captures, while in 22 traps approached from the front and one or more sides or the back 11 captures were made. These data obviously indicate a rather thorough investigation of the trap before entry in most cases. In the preliminary experiment bait was placed at the rear of the Sherman traps on a "bait hook" while in the later experiment the bait was placed about midway of the trap on the trap pan. This variation in procedure provided some evidence of attractiveness of the bait. Several approaches recorded in the preliminary trapping period showed evidence of much activity near the rear of the trap close to the bait, but no approaches were registered near the trap entrance. Apparently the bait was sought after, but no attempts were made to investigate all sides of the trap in an effort to obtain the bait. Placement of bait in a trap thus might spell the difference between trap success or trap failure.

In view of the many mammal population studies completed and in progress, there seems to be a dearth of direct evidence confirming or refuting the possibility of an initial reaction to a trap by mammals in its vicinity. In the absence of positive evidence, it is most often assumed that a mammal encountering a trap exercises a choice and responds either positively or negatively. This inferred response has been variously called "trap response," "trap reaction," "trap attitude" or "new object reaction." Some direct observations of initial behavior responses have been made by Fowle and Edwards (1954) with captive shrews confined in a small pit and by Thompson (1953) in an experimental colony of wild rats. Whether similar behavior would be observed under natural conditions allowing unrestricted movement is problematical. Any direct evidence resulting from visual observations would tend to be limited to relatively few individuals under natural conditions and observance of nocturnal species would be impractical.

Formulas used for computing population size from recapture of marked animals are generally based upon the assumption that the probability for recapture of all marked and unmarked individuals in a population is the same and is unaffected by traps or trapping procedures. This assumption has been at least partially disproved by Young *et al.* (1952) and our own study shows that such an assumption could be false.

The use or modification of the method employed in this study might end some of the speculation concerning trap responses by investigators of mammal populations. In confined populations of known size (Strecker and Emlen, 1952; Southwick, 1955) with all mice individually marked, many of the uncertainties encountered with natural populations would be eliminated and assumptions as to the probable size, composition and density of the population would be unnecessary.

Results of a few field trials have shown that rain and wind tend to obscure records of tracks on sooted paper. The method of study here reported therefore would be of optimal value in dry situations or under indoor conditions. It is possible, however, that some sort of trap shelter might be devised which would protect the paper from rain without blocking the approach of a mammal to the trap.

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BREEDING-BIRD POPULATIONS OF STRIP-MINED LAND IN PERRY COUNTY, ILLINOIS

Published material concerning the vegetation of strip-mined areas is plentiful, but little attention has been paid to animal communities of these areas. The present study was concerned with bird populations of a tract of land strip-mined for coal between 1932 and 1950. The bird species occupying the tract and their relative abundances were determined. Changes in the bird population with respect to time were studied by apportioning field work into five time-since-stripping classes of 6-9, 10-13, 14-17, 18-20, and 21-24 years.

Part of the field work was done while the writer was a research assistant on Project 26, Cooperative Wildlife Research Laboratory, Southern Illinois University. The manuscript was completed during the tenure of a National Science Foundation fellowship. Particularly helpful comments on the manuscript were made by S. C. Kendeigh, J. W. Hardy, W. D. Klimstra, and R. M. Mengel. Statistical advice was provided by H. W. Norton. Appreciation is due the University of Illinois Statistical Service Unit and the Digital Computer Laboratory for use of their facilities.

Description of the Study Tract

The study was conducted on a 1792-acre tract in Perry Co., Illinois, about five miles southwest of Pinckneyville. Although certain features of areas stripped recently and those mined 23 to 24 years previously were different, the general aspect of the tract was fairly uniform (Brewer and Triner 1956: 76-80). The topography was that of alternate valleys and ridges, with an average relief of about 30 feet. Many valleys contained water permanently or during some parts of the year, and lakes up to 15 acres were present in the deep valleys which represented the final path of mining equipment in each section. The vegetation consisted of wide-spaced trees, mainly cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), and elms (*Ulmus americanus* and *U. rubra*). As a result of the wide-spacing (mean distances between trees of random pairs: 16-45 meters), tree crowns did not form a canopy anywhere on the tract. Between the trees, the ground was rather sparsely covered with ruderals (mean density about 53 stems per square meter). These included white sweet clover (*Melilotus alba*), goldenrod (*Solidago ulmifolia*), common ragweed (*Ambrosia artemisiifolia*), aster (*Aster pilosus*), and cheat (*Bromus secalinus* and *B. tectorum*). Sandbar willow (*Salix interior*) formed fairly dense thickets in valleys throughout the tract. Marginal vegetation of ponds and lakes (Bell 1956: 87) consisted of willows (*Salix* spp.), cat-tail (*Typha latifolia*), or moist soil annuals (such as *Echinocloa crusgalli, Polygonum pennsylvanicum,* and *Cyperus ferruginescens*).

Four features were noticeably associated with time since stripping. The size of trees increased from 10 feet high on lands stripped 6 years to 65 feet high on lands stripped 23-24 years. As a result of the attendant increase in shade, light intensity was lower on the earliest-stripped lands. Taken with a Weston illuminometer with a Viscor filter, readings ranged from 3120 to 6400 foot-candles on lands stripped 6 years and from 2120 to 5210 in comparable situations on lands stripped 23-24 years. Aside from sandbar willow, dense growths of small trees, shrubs, and woody vines were absent on lands stripped less than 8 to 10 years. Finally, numerous elm saplings appeared in areas stripped more than 18 or 20 years. Their presence suggests the possibility of denser tree growth and a closed canopy in the future.

Procedure

Indices to the bird populations were obtained by means of one-hour cruises, each restricted to lands stripped during two consecutive years. All birds encountered along a roughly rectilinear course were recorded. The abundance of each species was expressed in equivalent pairs, with each individual or pair of obviously mated individuals representing one equivalent pair. Twenty cruises were taken from June 30 to July 27, 1954, and June 8 to July 11, 1956 (Table I). Cruises on later dates encountered young birds and were considered with informal observations made from June 23 to August 4, 1954, and at other times during the two succeeding summers. The cruises were taken during the morning hours (extreme times of beginning: 6:15—11:10 CST), and an effort was made to standardize distance covered and intensity of observation. The possibility that efficiency of the sampling unit varied according to time of day and season was examined in the statistical treatment given the data. Analysis was by the method of least squares, using a model which included a constant for the difference between the two observational years, polynomial effects of the third degree for time of day and for season, and a polynomial effect of the fifth degree for time since stripping. Neither time of day nor season, tested by the usual F test, were significant at the 5 percent level.

Table I. Numbers of cruises, total bird species, and mean equivalent pairs for five time-since-stripping classes of Perry Co., Illinois, striplands

	Years Since Stripped				
	6-9	10-13	14-17	18-20	21-24
Cruises	5	5	4	3	3
Species	21	25	32	31	28
Equivalent pairs/hour	22.4	28.2	39.7	31.3	31.2

Composition of the Bird Population

Forty-eight species were recorded on the tract. Four of these, common egret (*Casmerodius albus*), little blue heron (*Florida caerulea*), purple martin (*Progne subis*), and barn swallow (*Hirundo rustica*), were eliminated from further consideration because they did not breed on the tract. The most numerous species, in order of decreasing abundance, were field sparrow, indigo bunting, mourning dove, cardinal, redwinged blackbird, rufous-sided towhee, Am. goldfinch, yellow-breasted chat, and yellow-billed cuckoo (Table II). These nine species each had a mean abundance for all areas of more than one equivalent pair. The mean number of species seen during one hour was 13 for all areas, and the mean number of equivalent pairs was 30.0 ± 2.0.

Nearly all of the 44 breeding species are among those classified as forest-edge birds. V. R. Johnston (1947: 45) has defined forest-edge birds as those species which are confined to the border of the forest or which use both the forest and the surrounding field in their activities. D. W. Johnston and Odum (1956: 57) state that forest-edge species are those which require for their breeding territories two or more communities of widely different

ecological ages intermixed. Neither definition seems adequate in the case of the striplands populations. Johnston's definition fails to provide for areas where there is no particular relationship to any forest. Johnston and Odum's definition becomes more comprehensible when amplified by their subsequent statement (1956: 58) that ". . . a forest edge community is a mixture of early and late successional stages (grass and trees or grass, shrubs, and trees). . . ." However, their implication that trees are ecologically older than grasses or shrubs seems based on a stereotyped view of succession as a process which follows a predetermined pattern, as from bare ground, to annual herbs, to perennial herbs, to shrubs, to trees. On the striplands, trees and herbs had evidently invaded about the same time, within a year after stripping.

A more realistic definition of forest-edge species might attempt to use as its basis the actual feature or features of the environment to which the organisms respond. With birds, at least, this feature appears to be the physiognomy of the vegetation. The simplest realistic definition appears to be that forest-edge species are those which tend to occur where there is an interspersion of trees and/or shrubs in areas covered by herbaceous plants.

One should remember that a term such as forest-edge species is merely a convenient generalization and that organisms tend to occur wherever their niche requirements are satisfied. So-called forest-edge species may occur in areas which would never be considered forest-edge: Johnston's report (1947: 51-52) of the occurrence of house wrens and indigo buntings throughout two mature mesophytic forests is a good example. Likewise, vegetation which one may choose to classify as forest edge may fail to support populations of birds generally regarded as forest-edge species and may support populations of birds not so regarded. On the striplands, such typical forest-edge species as brown thrashers, catbirds, and yellow-breasted chats were lacking on lands stripped less than 8 or 10 years. Their absence in more recently stripped areas can probably be explained by the lack of a low, dense, plant cover, which they presumably require. On the other hand, lark sparrows, blue-gray gnatcatchers, Carolina wrens, and red-eyed vireos are not regarded as forest-edge species, but all occurred on the tract, evidently finding conditions such that their respective niche requirements were satisfied.

Changes in the Bird Population with Time

Differences in the bird populations of lands stripped in different years seem to be explainable on the basis of responses of individual species to two factors: vegetational changes related to time since stripping and local site conditions.

Bird density appeared to be related to time since stripping, with the greatest number of equivalent pairs occurring in lands stripped 14-17 years (Table I). The apparent differences, however, were not significant at the 5 percent level. Local variation in vegetation may have been most important in determining density.

Local conditions were primarily responsible for the presence of at least three species. Belted kingfishers were present where there were fairly extensive bodies of water with steep banks. Redwinged blackbirds were associated with growths of cat-tail. Ultimately, the occurrence of both species depended on mining conditions and water-table level. Killdeers nested only on the packed gob roads used by mining trucks. These roads were intact throughout the time sequence studied, although eventual invasion of vegetation may make them unsuitable for the species.

The presence of certain other species seems related to successional changes in the vegetation. The development of low, dense, shrubby growth favoring brown thrashers, catbirds, and yellow-breasted chats has already been mentioned. The occurrence of woodpeckers, parids, house wrens, and eastern bluebirds was probably dependent on

Table II. Mean abundance (equivalent pairs per hour) of forty-four species of birds for five time-since-stripping classes of Perry Co., Illinois, striplands. Species marked X occurred in the class indicated but either were not recorded on one of the formal cruises or had a mean abundance of 0.5 or less

Species	Years Since Stripped					
	6-9	10-13	14-17	18-20	21-24	Mean
Green Heron, *Butorides virescens*	X	..	X	..	..	X
Red-tailed Hawk, *Buteo jamaicensis*	X	..	X	X	X	X
Bobwhite, *Colinus virginianus*	X	X	1	X	1	X
Killdeer, *Charadrius vociferus*	..	X	X	..	..	X
Mourning Dove, *Zenaidura macroura*	1	3	2	1	1	2
Yellow-billed Cuckoo, *Coccyzus americanus*	1	2	2	1	2	1
Black-billed Cuckoo, *Coccyzus erythropthalmus*	..	..	X	.	X	X
Belted Kingfisher, *Megaceryle alcyon*	..	X	X	..	..	X
Yellow-shafted Flicker, *Colaptes auratus*	..	..	X	X	..	X
Hairy Woodpecker, *Dendrocopus villosus*	..	X	..	..	..	X
Downy Woodpecker, *Dendrocopus pubescens*	X	..	..	..	1	X
Eastern Kingbird, *T. tyrannus*	X	1	1	X	..	X
Wood Pewee, *Contopus virens*	..	..	X	X	1	X
Blue Jay, *Cyanocitta cristata*	1	1	X	X	..	X
Common Crow, *Corvus brachyrhynchos*	X	..	..	..	1	X
Carolina Chickadee, *Parus carolinensis*	..	..	1	1	X	X
Tufted Titmouse, *Parus bicolor*	..	..	X	1	..	X
House Wren, *Troglodytes aedon*	..	..	..	..	X	X
Carolina Wren, *Thryothorus ludovicianus*	..	..	X	X	1	X
Catbird, *Dumetella carolinensis*	X	X	1	X	1	1
Brown Thrasher, *Tozostoma rufum*	1	1	X	X	1	1
Eastern Bluebird, *Sialia sialis*	..	..	X	X	X	X
Blue-gray Gnatcatcher, *Polioptila caerulea*	..	X	..	X	..	X
Cedar Waxwing, *Bombycilla cedrorum*	..	X	X	X	X	X
White-eyed Vireo, *Vireo griseus*	..	..	..	1	X	X
Bell's Vireo, *Vireo belli*	..	X	X	..	..	X
Red-eyed Vireo, *Vireo olivaceus*	..	..	..	..	X	X
Warbling Vireo, *Vireo gilvus*	X	1	1	X	1	1
Prothonotary Warbler, *Protonotaria citrea*	..	..	X	X	..	X
Yellow Warbler, *Dendroica petechia*	..	X	..	1	..	X
Prairie Warbler, *Dendroica discolor*	..	..	..	1		X
Yellowthroat, *Geothlypis trichas*	..	..	..	X	.	X
Yellow-breasted Chat, *Icteria virens*	..	1	3	3	2	2
Redwinged Blackbird, *Agelaius phoeniceus*	3	2	3	X	X	2
Orchard Oriole, *Icterus spurius*	X	X	X	X	X	X
Baltimore Oriole, *Icterus galbula*	..	..	..	..	X	X
Brown-headed Cowbird, *Molothrus ater*	..	X	X	..	X	X
Cardinal, *Richmonaena cardinalis*	1	2	4	2	1	2
Indigo Bunting, *Passerina cyanea*	3	3	6	6	5	5
Am. Goldfinch, *Spinus tristis*	1	2	2	1	1	2
Rufous-sided Towhee, *Pipilo erythrophthalmus*	2	2	1	2	3	2
Lark Sparrow, *Chondestes grammacus*	X	..	..	..	..	X
Field Sparrow, *Spizella pusilla*	4	5	6	5	5	5
Song Sparrow, *Melospiza melodia*	1	1	1	X	..	1

dead trees of sufficient size for nesting activities. Singing and nesting sites of suitable height and the development of tree crowns to provide some minimum amount of shade may both have been important factors in the appearance of the various warblers and vireos (*cf.* Kendeigh 1945: 422-32). Shade and the development of fairly large horizontal limbs for nesting are probably requirements of the wood pewee (Saunders 1942: 184).

The changes in species composition with time, although not great, appear to be in the direction of loss of field and forest-edge birds and addition of more typically forest-inhabiting species. Future changes of this sort will probably depend on the production of a closed canopy. This event may be expected with the growth of elms and other trees which have invaded among the cottonwoods.

Summary

Bird populations of Perry Co., Illinois, lands stripped for coal between 1932 and 1950 were studied during the breeding seasons of 1954-56. The lands stripped during various years were similar, consisting of alternate ridges and valleys supporting wide-spaced trees and a ground cover of ruderals. Increasing tree size, increasing shade, and the appearance of dense, shrubby growth and elm saplings were associated with increasing time since stripping. Forty-four breeding species were recorded. Most abundant were field sparrow, indigo bunting, mourning dove, and cardinal. Most of the recorded species may be classified as forest-edge birds; that is, they occur where there is an interspersion of trees and/or shrubs in an area covered by herbs. Differences in the bird populations of land stripped in different years were the result of responses of individual species to successional changes in vegetation and to local site conditions. Future successional changes in the bird population, involving replacement of field and forest-edge birds with forest species, will probably depend on the development of a closed canopy.

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THE EPHESTIA-IDECHTHIS ECOSYSTEM FOR ILLUSTRATING POPULATION DYNAMICS

When a population is under natural control its density usually, if not always, governs the action of the controlling agent (Nicholson 1933). This relation is exemplified most easily and clearly by the host-parasite interaction, provided, of course, that this interaction holds the host population at levels below the limit fixed by its food supply. The demonstration of such an interaction and the elucidation of the population dynamics involved requires continually self-perpetuating populations of both the parasite and its host. Prior to the situation here reported, this requirement has not been attained, the nearest approach to attainment being that described by Burnett (1943, 1949). Burnett experimented with populations of the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood) and its parasite *Encarsia formosa* Gahan. He noted that under greenhouse conditions the populations of these insects form a relatively well-defined system and that the two species show mutual adaptations for the preservation of the system. The experimental use of the system, however, is greatly handicapped by the inclusion of living plant tissue for the sustenance of the whitefly populations.

Preliminary studies by the writer (Flanders 1948) have shown that self-perpetuating populations of the moth *Ephestia kühniella* Zeller and the wasp *Idechthis canescens* (Gravenhorst) subsisting on a continuously available basic resource (rolled wheat) may be used to illustrate the basic ecological factors governing populations with a precision and interpretative significance otherwise unattainable. Consequently, in 1956 a program for studying such a system was initiated in the Department of Biological Control laboratories of the University of California at Riverside.

This host-parasite interaction and its environment is in fact an ecosystem since they form a complete biotic community within a particular physico-chemical system. It is a permanent and self-sustaining community excepting that the supply of basic resource is sustained artificially.

With a series of such ecosystems under controlled conditions it will be possible to analyze and evaluate the role of temperature, humidity, light, nutrition, dispersion, and protection from enemies on the population equilibrium positions.

Any change in population densities resulting from the deviation of a single ecological factor from that in the ecosystem selected as standard can be readily assessed. Differences in the "food-searching" capacities of host and of parasite are subject to analysis.

The Ephestia-Idechthis ecosystem is especially suitable for such a study because the basic resource, rolled wheat, is a non-living standardized constant, and both animals, *Ephestia* and *Idechthis*, are naturally adapted to continuous reproduction with enclosures such as can be set up in the laboratory.

The Ephestia-Idechthis ecosystem as established in the laboratory appears comparable to similar ecosystems under outdoor conditions. The obvious differences other than in size are not likely to invalidate conclusions drawn from laboratory studies. These differences involve the manipulation of the host population to form a continuous

succession of episodes, each episode being a set of distinctive developmental events in the life of the ecosystem. This is accomplished by the regular replenishment of the basic resource (rolled wheat) in measured amounts. The extent to which this resource is utilized depends on the relative self-determined densities of host and parasite populations.

When the ecosystem is suitably housed, the interacting populations can attain their full potentialities, static and dynamic. Within each ecosystem the status of the population is a function of the habits of *Ephestia* in conjunction with the habits of *Idechthis*, not of the amount of the basic resource. The population of *Idechthis*, however, may be considered a function of its food supply since in number of individuals it approaches or equals the number of *Ephestia* larvae that invaded its area of search.

The original housing of each ecosystem of the planned series encloses about 1/8 cubic meter (4.5 cubic feet) of space, and the rolled wheat occupies 24 stender dishes evenly spaced on the cage floor (see Figure 1). When the temperature is constant at 25° C and the relative humidity between 50 and 55 percent, six months are required for the system to develop to a state of equilibrium. The attainment of a relatively constant steady density of the population requires about one year.

FIG. 1. Interior of a glass-covered cage housing an Ephestia-Idechthis-rolled wheat ecosystem. The episodes in the life of this ecosystem occur within the stender dishes. The relative ages (in weeks) are shown by the numbered squares.

Note that a glass cylinder when in posititon increases the minimum traversable distance between dishes.

The procedure in attaining equilibrium involves the following steps:

(1) The floor of the cage is marked into 24 equal squares which are numbered 1 to 24 but without adjacent squares having numbers in sequence.

(2) A stender dish containing approximately 8 grams (120 grains: Troy weight) of rolled wheat, 14 mm in depth and 43 mm in surface diameter, is placed in one of the squares.

(3) A mated female *Ephestia* is placed in the system with the stender dish of wheat.

Step number (2) is repeated at weekly intervals until all the squares in sequence, 1 to 24, contains a stender dish of wheat.

Step number (3) is repeated until the first moth completes its development.

As the wheat in each stender dish becomes infested it forms an episode in the life of the ecosystem. The *Idechthis*, after its introduction, forms a part of each episode; the first *Idechthis* female being introduced when the fourth square receives its stender dish of wheat. Thereafter an *Idechthis* female is introduced as the preceding one dies until the beginning of *Idechthis* emergence.

At the end of six months, when the 24th dish has been in the system for one week, the initial, stender dish is exhausted and removed. The perpetuation of the ecosystem requires the replacement of each dish as it becomes exhausted with a stender dish of fresh wheat. (In the absence of *Idechthis* the wheat in a dish may be completed exhausted by *Ephestia* in one month.) Since the individual *Idechthis* consists of the converted body of an individual *Ephestia* and consequently represents it in the ecosystem, the total host population, as well as the percentage parasitization in each ecosystem, can be accurately measured by means of the dead adults of both species.

The amount of unused wheat in an exhausted stender dish in which population oscillations occurred at minimum amplitudes is about one-fifth of the original supply. This proportion of wheat is unused because it formed part of the areal (volumetric) range searched by the parasite. This range is predetermined by the spatial dimensions of the system, the distance between the dishes, the surface area of the wheat, and the length of the parasite ovipositor.

However, as pointed out by Nicholson and Bailey (1935), the efficacy of a parasite in controlling its host is a function of its "area of discovery." The value of this area of discovery is determined partly by the searching capacity of the parasite and partly by the movement, size, spoor, and accessibility of the host.

In the Ephestia-Idechthis ecosystem the areal range is artificially regulated and constant for each ecosystem. Consequently, it is the area of discovery which regulates for each ecosystem the amount of parasitization and degree of population control. It is the more or less continuous movement of the *Ephestia* larvae into and out of the top 15 percent of the infested wheat that permits such regulation. This movement is a constant feature of all episodes so that each larva at some period of its life is exposed to attack by the parasite population.

The percentage of parasitization therefore is a function of the frequency with which the parasite searches the host-inhabited area correlated with the rate at which the larval host population moves in and out of the areal range of the parasite population.

Before the populations of any ecosystem attain their steady densities, the wheat in one or more of the dishes may be completely destroyed by a population that is 98 percent parasitized. It is under such conditions, however, that within a single dish 90 hosts may complete their larval development.

During the first two months of the second year in the life of the initial ecosystem, approximately 77 *Ephestia* larvae cocooned each week, the weekly parasitization ranging from 54 to 70 percent and averaging 61 percent. A total of about 77 larvae cocooned in each dish, although the total amount of wheat in each is sufficient for the complete development of 90 such larvae.

When an ecosystem such as that described above is well established, approximately 4,000 *Ephestia* larvae cocoon annually at the rate of about 5 to 15 per day. Since the annual production of *Ephestia* adults is estimated to be less than 5 percent of their inherent reproductive capacity the surplus progeny of the *Ephestia* population is relatively very large.

At a temperature of 25° C there are approximately 8 generations of *Ephestia* and 12 generations of *Idechthis*

annually, each dish yielding 6 generations of the parasites and 4 generations of the host. The reproducing adults are unfed, the life of the parasite then being about 3 days; that of the host 7 days (Ahmad 1936).

The distance between dishes affects the searching capacities of the host and parasite populations. This distance can be increased several feet by placing sections of tubing over each dish (see Figure 1). Greater distance can be attained by transferring an entire set of dishes in equilibrium to a larger environment. The area of discovery may be changed by changing either the surface area of the wheat or its depth.

In an ecosystem in equilibrium it is apparent, as pointed out by Latham (1952), that the host controls the population of its parasite by its accessibility, its quality as food, and its influence on fertility at the same time that the parasite acts as a brake against the suicidal expansion of the host population.

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A NOTE ON THE PHYTOPLANKTON-ZOOPLANKTON RELATIONSHIP

The zooplankton and phytoplankton pulses are generally considered to be coincident or immediately following each other. Annual and seasonal cycles seem to be of a highly variable nature from lake to lake and from year to year within the same lake. Each body of water is distinctive and should be meticulously studied as an individual case (Pennak 1946). With regard to the dependence of the rotifers upon their food phytonannoplankton ("Zentrifugenplankton") in a small pond in Germany, classical work was made by Dieffenbach and Sachse (1912).

But there are many papers in which different authors give examples of irregularities, particularly concerning the phytoplankton-zooplankton relationship. The most interesting cases are these of the inverse correlation between the density of the two main groups of plankton. An intuitive example was given by Anderson, Comita and Engstrom-Heg (1955) for two saline lakes in Washington having an area of 336 ha. and 556 ha., respectively, and a maximum depth of 26 and 11 m. The high salt content limiting the qualitative composition of the plankton made the work easier and the general survey more clear. The authors concluded that "a control of phytoplankton population size by the grazing activity of the zooplankton is given as the most probable interpretation of the seasonal changes observed."

This note has to contribute to the knowledge of this problem in another kind of water body, *i.e.* in a small lagoon of highly eutrophic character, which served through two seasons for the purification of wastes from a beet-sugar factory.

It was a fishpond situated below the sugar factory at Vinoř near Prague, Czechoslovakia, which was emptied in the autumn of 1949. All industrial wastes, produced by the factory during the campaign, were drained into this lagoon having an area of 1.5 ha., a volume of 17,000 cbm. and a maximum depth of 2.3 m. The wastes were treated twice with lime and the originally anaerobic conditions were changed at the end of February 1950 after the thawing of ice into aerobic ones, caused chiefly by the photosynthesis of a phytoplankton community, composed of *Chlamydomonas, Chlorogonium* and *Euglena*. It can be stated in terms used in saprobiology that the polysaproby was changed into alpha-mesosaproby. In different depths up to 22,000 cells per cc. were counted. No net zooplankton was observed during and after this pulse of phytoplankton.

In the second half of April a second phytoplankton pulse was formed by several species of the genus *Cryptomonas* (*C. rostrata, C. pyrenoidosa, C. ovata, C. marssonii*) and accompanied by *Ankistrodesmus convolutus*. The greatest density, found near bottom was 20,000 phytoplankter per cc. As late as at this time the zooplankton appeared, represented originally by the rotifer *Epiphanes senta* and followed by *Brachionus calyciflorus, B. rubens* and further by *B. urceolaris, Polyarthra vulgaris* and *Asplanchna brightwelli*. The crustaceans were present in small numbers only (*Daphnia longispina, Ceriodaphnia quadrangula*, nauplii and cyclopids). The maximum number of rotifers counted was 6,500 per liter. At this time young carp were introduced into the lagoon and the lagoon was to be considered as a normal fishpond again.

After the retreat of the *Cryptomonas* population in the middle of May and following the minimum of the phytoplankton, a new (third) phytoplankton community formed in the last days of May, achieved its peak in the middle of June with more than 90,000 organisms per cc., then decreased and terminated in the second half of July. This large community can be named as a Chlorophycean one, because of the dominance of such forms as *Chlorella, Coelastrum, Oocystis, Scenedesmus, Pediastrum, Ankistrodesmus, Crucigenia* and others. The days of the maximum of the Chlorophycean phytoplankton were characterized by the absolute minimum of rotifers and by the decline of the peak of crustaceans which preceded the development of the Chlorophyceae. As late as at the end of June a resurgence of the zooplankton was observed. The increase reached its peak in the middle of July, also at the time when the Chlorophycean plankton was disappearing. The main members of this second pulse of the zooplankton were the rotifers *Brachionus angularis*

bidens, Polyarthra vulgaris, Pompholyx sulcata, Keratella cochlearis, K. quadrata, Filinia longiseta and *Hexarthra mira.* On July 10th and July 25th, 1950 the rotifers reached a density of more than 23,000 individuals per liter! (By contrast, Ahlstrom, 1933 counted in Terwilliger's pond, Put-in-Bay, Ohio, a maximum abundancy of 4,619 individuals per liter on June 10th, 1933.) The crustaceans *Daphnia longispina, Bosmina longirostris, Ceriodaphnia quadrangula, Cyclops vicinus* and the larva of *Chaoborus crystallinus* were present in moderate numbers.

After the decline of the Chlorophycean plankton two further feeble pulses of phytoplankton were noted, but the general trend was that of decrease. The first of these two resurgences was formed by *Eudorina elegans, Microcystis flos-aquae* and *Melosira granulata* during the second half of August. After a following period of minimum a new (fifth) phytoplankton community appeared in September with *Cryptomonas ovata, C. erosa, C. marssonii* and *Chroomonas caudata* as leading forms.

Among the zooplankton a pulse of *Keratella cochlearis* in August with 3,400 individuals per liter was relieved by another pulse with many species present but without a distinct dominance of any of them.

The further course of the development of the plankton communities was interrupted by drainage of the fishpond for harvesting the carp.

Survey

After the thawing of the ice cover five pulses of the phytoplankton were ascertained having the following peaks of population abundance:

1. In the first half of March (*Chlamydomonas, Chlorogonium, Euglena*), total maximum abundance 22,000 per cc.
2. In the first days of May (*Cryptomonas, Ankistrodesmus*), 20,000.
3. In the middle of June (*Chlorophyceae*), 90,000.
4. In the second half of August (*Eudorina, Microcystis, Melosira*), 5,500.
5. In the middle of September (*Cryptomonas, Chroomonas*), 3,600.

During the same period only four pulses of rotifers were determined, the last two being inexpressive:

1. In the second half of May (*Brachionus, Polyarthra, Asplanchna*), total maximum abundance 6,500 individuals per liter.
2. In the month of July (*Brachionus, Polyarthra, Pompholyx, Keratella, Filinia, Hexarthra*), 23,900.
3. In the second half of August (*Keratella cochlearis*), 4,700.
4. In the middle of September (*K. cochlearis, Asplanchna, Polyarthra*), 1,400.

The crustaceans had only one maximum:

1. From the second half of May till the first third part of June (*Ceriodaphnia, Bosmina, Daphnia*, nauplii, cyclopids), total maximum abundance 1,520 individuals per liter.

Discussion

Figure 1 shows the relationship of phytoplankton (N) and planktonic rotifers (R) in Lohmann's curves to the water temperature in degrees centigrade.

Because of their absolute absence, no pulse of rotifers or crustaceans corresponds to the first pulse of phytoplankton.

To the second pulse of phytoplankton there corresponds, with retardation of approximately a fortnight, the first pulse of rotifers and, with a retardation varying from a fortnight up to one month, the single maximum of crustaceans.

To the third pulse of phytoplankton (*Chlorophyceae*) there corresponds the second maximum of rotifers with a retardation of three weeks approximately.

The less expressive fourth and fifth pulses of phytoplankton did not result in any distinct pulse of the zooplankton which was present in some increased numbers only.

In the eutrophic small water bodies the dynamics of the pelagic species during the warm season may be more rapid than in large water bodies (e.g. the two saline lakes in Washington according to Anderson *et al.* 1955) and the populations reach higher peaks of abundance (*cf.* Ahlstrom 1933, Carlin 1943).

There is a difference between the perennial species and the uniseasonal ones, the last lacking the possibility of developing at any time and having, therefore, more expressive pulses at the convenient time, if no interference occurs.

If a zooplankton pulse follows the pulse of phytoplankton, it is evident that the grazing effect of the herbivorous zooplankton contributes considerably to the decline of the algae.

In the described case of the lagoon at Vinoř the phytoplankton was twice in advantage and it was able to develop undisturbed because of the absolute absence of the net zooplankton. The third greatest pulse of the phytoplankton started at the time of a minimum of rotifers and of a decrease of crustaceans and reached its peak at the time of zooplankton minimum. When the zooplankton were at a maximum, no pulse of phytoplankton developed. In the presence of moderate numbers of the zooplankton, only feeble pulses of the phytoplankton were able to develop. The retardation of the zooplankton pulses may be explained by slower reproduction and the necessity of phytoplankton for food.

These facts show that the grazing effect of the herbivorous zooplankton is sufficient to limit the phytoplankton population in time as well as in quantity, as stated by Harvey *et al.* (1935). The concept of Harvey and other authors, as summarized in Harvey (1945), may be more convenient to explain the phytoplankton-zooplankton relationship in freshwater than the "hypothesis of animal exclusion" of Hardy and Gunther (1935).

The described observations of the conditions in the lagoon near Prague are given on the basis of material which will be published in details in another place (Sládeček *et al.* in press).

Summary

1. During the period October 1949 to September 1950 the author studied the changes of the quality of the phytoplankton and zooplankton in a fishpond of 1.5 ha. at Vinoř near Prague (Czechoslovakia) which served as a lagoon for the biological treatment of industrial wastes from a beet-sugar factory.

2. After the successful self-purification aided by treating twice with lime, conditions normal for eutrophic fishponds arose and pulses and minima of plankton were noted. A rich stock of nutrients for the phytoplankton was available. Five pulses of the phytoplankton were observed and compared with four of the planktonic rotifers and with a single one of the entomostraca.

3. The pulses of the zooplankton depended upon the pulses of the phytoplankton and were retarded for a fortnight up to one month.

4. Three great phytoplankton pulses started in the complete absence of or at the minimum of the zooplank-

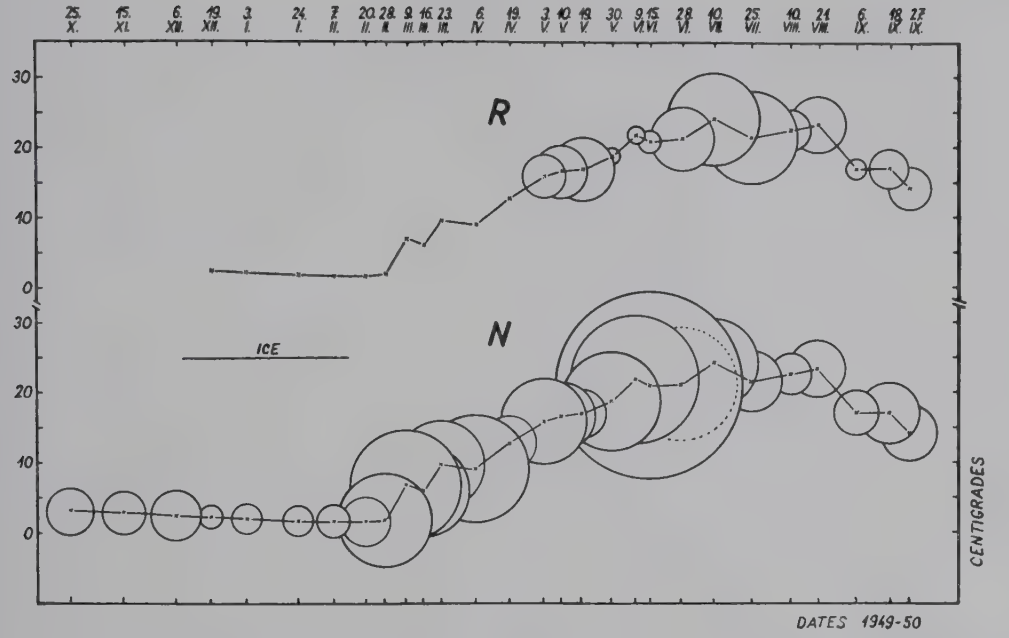

FIG. 1. The seasonal variations and the phytoplankton-zooplankton relationship in a 1.5 ha. fishpond at Vinoř. Phytoplankton = N, rotatorioplankton = R, the third axis being that of the water temperature. The quantity of individuals is given in Lohmann's curves. For the quantity of plankton organisms average numbers for the total water column were used, *i.e.* for the depths 0.1 m, 0.5 m, 1.0 m, 1.5 m, and 2.0 m.

ton. The two additional feeble phytoplankton pulses in late summer and autumn were accompanied by sizable numbers of zooplankton and were not able to develop in such a way as the preceding three.

5. Harvey's opinion, that the grazing activity of the zooplankton controls the size of the phytoplankton population, is the most convenient explanation for the seasonal changes observed in the studied lagoon.

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FURTHER OBSERVATIONS ON SELF-FERTILIZATION IN CHTHAMALUS SP.[1]

There is little doubt that obligatory cross-fertilization is common throughout the operculate species of barnacles, but contrary to a previous view (Crisp, 1950) is has been shown recently that some species although normally cross-fertilizing may, in the absence of contiguous individuals, self-fertilize (Barnes and Crisp, 1956). This has been shown to be the case in *Chthamalus stellatus*, *Balanus perforatus* and *Verruca stroemia* the first two being intertidal and the third largely a sublittoral species. In the case of *Chthamalus stellatus* self-fertilization, although apparently less efficient than cross-fertilization appears to produce viable nauplii; clearly there is a survival value in self-fertilization particularly evident in *Chthamalus stellatus* where isolated individuals occur high up the shore.

During the course of ecological work along the American coasts the opportunity has been taken of examining other species of *Chthamalus* for evidence of self-fertilization. It was not possible to follow the development of broods throughout a season but samples of the species were taken in a restricted area as opportunity arose.

In each case twenty well grown contiguous individuals were taken and twenty individuals separated by at least 5 cm.; the state of the ovary and embryos were recorded. The places of collection and species concerned are listed below.

East Coast: (a) Rocky Beach, Woods Hole, Mass., *C. fragilis* Darwin. West Coast: (b) Will Rogers Beach, Santa Monica, California, *C. fissus* Darwin; (c) Big Rock, Malibou Beach California, *C. fissus;* (d) Charleston, Coos Bay, Oregon, *C. dalli Pilsbry;* (e) Anacortes, Washington, *C. dalli;* (f) San Juan, Outer coast, Washington, *C. dalli.*

The results are given in Table I which shows the percentage of the animals with their gonads in various states of development.

It is evident that in all three species at all the places investigated isolated individuals bear ripe embryonic masses. These appeared to be normal and in all cases (except Woods Hole where pickled material was examined) were capable of giving active and apparently viable nauplii. There is again evidence that self-fertilization is delayed beyond the time at which cross-fertilization would have occurred.

[1] Contribution No. 949 from the Woods Hole Oceanographic Institution.

TABLE I. Comparision of separate (sep.) and contiguous (con.) individuals, *Chthamalus* sp.

Place	Date	Condition (%)							
		Empty or unfertilized		Early stage embryos		Limbed embryos present		Eyed nauplii present	
		Sep.	Con.	Sep.	Con.	Sep.	Con.	Sep.	Con.
(a)	1/7/57	45	35	20	35	5	15	30	15
(b)	11/4/57	100	100	0	0	0	0	0	0
	3/6/57	50	35	0	0	40	35	10	30
	17/6/57	35	25	35	5	15	55	15	15
(c)	3/6/57	95	85	0	0	0	5	5	10
(d)	29/6/57	30	25	25	45	5	10	40	20
(e)	3/7/57	75	40	15	5	0	0	10	5
(f)	2/8/57	75	45	15	50	0	0	10	5

It would seem that facultative self-fertilization is common in the genus perhaps extending to all species.

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META-MODELS IN THEORETICAL ECOLOGY

In the development of ecology there are two types of theoretical formulations that can be made.

It is possible to construct an equation or system of equations, the terms of which will all have a specific biological meaning, which is designed to behave in the same way as some particular real or hypothetical biological system. For example, it is possible to write an equation in which some variable will change as a function of time in the same way as does the number of beetles in a flour beetle culture. It is also possible to use a set of reasonable physiological assumptions to construct an equation which predicts a community structure or population history which does not correspond to anything in the discovered real world, and represents a hypothetical future discovery. Such equations or systems of equations are models of nature.

It is clearly possible to construct at least as many mathematical models as there are kinds of organisms. If we consider all possible models that are relevant to some particular area of ecology it is possible to sort these models into categories, or into some orderly sequence on the basis of either quantitative or formal properties. Such a categorization of models will be called a meta-model. It is the contention of this note that the construction of meta-models will be of greater significance in the advance of theoretical ecology than will the construction of specific models.

Any mathematical model which succeeds in completely

describing a specific ecological phenomenon is usually complex and of very narrow applicability. Recently the number of published models has increased and the range of applicability of each model correspondingly decreased. This trend toward the construction of complex specific models may eventually make a unified theory of ecology almost impossible to attain unless some organization of specific models is possible.

An ecological model usually consists of a deterministic or stochastic equation which permits prediction of an ecological event once several constants have been determined. In the case of a stochastic model these constants may include variances associated with either the known parameters of the system or with an unspecified group of unknown properties. In this case predictions will also have a range of expected error associated with them, but a stochastic model is nevertheless as specific in area of applicability as a deterministic one.

Three examples of meta-models will be presented.

MacArthur (1955) has constructed a meta-model of community stability. If we consider all possible communities of organisms it is invariably the case that some members of each community eat or are eaten by others. That is, a food web diagram can always be constructed for a community. MacArthur can now rank all food web diagrams in order of stability on topological grounds. Other things being equal, MacArthur's criteria are universally applicable to all communities. He can show, among other things, that in a community with very few species, stability is very difficult to achieve, even if many trophic levels are represented in the diet of each species. Increasing the number of species, while keeping the number of trophic levels constant tends to increase community stability, thereby permitting dietary specialization.

Any model designed to predict the behavior of a specific community can simultaneously be ranked as to stability by MacArthur's criteria. However, two entirely different communities, with different actual stabilities may receive the same rank of stability in MacArthur's meta-model. In particular, there is ample field and experimental evidence that populations of single species also differ widely from each other in their tendency to fluctuate. Two communities which can be represented by identical food web diagrams may differ greatly in stability because one is composed of much more stable species than the other. In fact, some species can show fluctuations in population size, even when they are isolated from all environmental fluctuations.

Slobodkin (1955) has constructed a meta-model in which all single species populations, living in a spatially limited constant environment, can be divided into those for which population equilibrium is possible, those which show oscillation, and those which can maintain equilibrium if undisturbed but cannot return to equilibrium once their equilibrium is disturbed. The data required for this are age-specific fertility and mortality rates, and information on the density dependence of fertility and mortality. No particular population growth model is specified.

If we now rank a community as to stability on the basis of the MacArthur meta-model, and assign each species in that community to the appropriate category of the Slobodkin meta-model, we will be able to make some general prediction without ever constructing a specific model.

Ricker (1954) has constructed a meta-model in which he has confined his attention to single species populations in which population equilibrium is possible on the basis of survival and reproductive data, but in which equilibrium may or may not be likely actually to occur. That is, Ricker's meta-model further subdivides one of the categories of Slobodkin's meta-model. On the basis of the relation between the number of adults in the populations and the number of adults which produce them, Ricker can divide populations for which equilibrium is possible into four categories: those which come to equilibrium immediately, those which show damped oscillation, those which show undamped oscillation, and those which are unstable.

These three meta-models, while discussing different ecological problems, have the following common properties:

1) They all define an area of applicability and then subdivide or organize all the items in that area on the basis of simple criteria. MacArthur defines his area of applicability as all communities for which food web diagrams can be drawn and then ranks these communities in order of stability. Slobodkin defines his area as all single species populations for which fertility, mortality and density dependence data are available, and then categorizes these populations with reference to the possibility of population equilibria or oscillations.

2) A relatively small amount of information is required in assigning a particular ecological event to its appropriate rank or category in the meta-model. This is in contrast with the enormous amount of physiological data required for the development of specific deterministic models.

3) A single event may be assigned to its appropriate position in several meta-models simultaneously. For example, a population in a community may belong to the category of populations in which equilibrium is possible according to the Slobodkin meta-model, while belonging to the category which may be expected to undergo damped oscillation on the Ricker meta-model, and at the same time the food web of the community in which this population exists will be assigned some stability value by the MacArthur meta-model.

Analyzing a phenomenon on the basis of several independent meta-models may provide almost as good a basis for prediction as would the construction of a precise predictive model.

The whole meta-model approach is simply a series of classificatory criteria which permit us to make adequate predictions of particular phenomena without using theoretical equations of a directly predictive kind.

There has been a trend in theoretical ecology towards each investigator developing his own equations and systems as if he were alone in the field, ignoring or denigrating the work of other theoreticians. It seems possible that the meta-model approach will permit the activity of different theoretical workers to be additive, resulting in a unified body of ecological theory rather than a chaotic collection of erudite performances.

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EXPERIMENTAL NOTES ON THE DEEP SPRINGS TOAD *BUFO EXSUL*

During the spring of 1956 the writer, then an instructor at Deep Springs Junior College in Deep Springs Valley, Inyo County, California, initiated a series of studies toward an ecological life history of *Bufo exsul* Myers, a species endemic to this small valley. Although these studies were short-lived, some of the results obtained appear to be worth recording at this time, since it is most unlikely that the present writer will be able to continue with this project.

Nearly all that has been published concerning this toad is well summarized by Wright and Wright (1949: 176-180), along with a good description of its habitat. Very briefly, the species is to be found only in a series of springs at the south end of a small valley (as well as at one or two locations in the northern end, but in small numbers) whose floor has an elevation of about 5000 feet, which has only interior drainage, and is characterized by considerable aridity. The dominant vegetation is rabbitbrush (*Chrysothamnus*) on the floor, with pinyon-juniper woodland commencing at about 6000 feet elevation on the surrounding mountains. The toad appears to have been isolated here since the withdrawal of the pluvial period lakes from the Basin and Range province, of which this valley represents the western edge.

Little equipment was available at the time the experiments were carried out, and close control of conditions was impossible. Nevertheless, several tests of the limits of tolerance of both tadpoles and adults to heat and of the adults to desiccation were made. Most of the individual animals used were collected by Mr. Charles Lepley, then a student at the school.

Heat tolerance of tadpoles.—In these tests a 100 ml. beaker nearly filled with water and containing a large tadpole (about 5 cm. long and weighing approximately one gram) was suspended in a larger vessel of water, and the latter placed on a ring stand over a burner. Temperatures of the water in the smaller vessel were recorded periodically as heat was applied, and notes on the behavior of the animal were made concurrently. Initial temperatures for five tests were between 22° and 23.5° C., with maximum temperatures being attained in 12 to 15 minutes. Responses to increasing heat varied somewhat. In general the tadpoles were quiet at the beginning, became quite active as the heat reached about 30-35°, then showed marked sporadic activity, with short period of rest interspersed with period of rather violent movement, at temperatures up to 39° C. Heat shock apparently set in at about 40-41°, at which temperatures movement was mostly restricted to tail twitches or occasional gulps. One of the tadpoles was held at 40° for 1½ minutes before cooling, whereas the others were brought to a peak only for an instant and were then removed to cooler water. The highest temperatures to which they were subjected were 42°, 42°, 41.5°, 41°, and 40° (for the longer period). The two exposed briefly to temperatures of 42° did not recover. The other three gradually became active again, and were returned to a stock jar, where they behaved normally for about ten days, at which time the tank became contaminated and the whole group was lost.

Strictly comparable data in other species are not available. Prosser (1950: 344-348) cites figures indicating that toad tadpoles (species?) acclimated at 22-23° C. withstood a temperature of 37.4° C. for one hour, whereas others reared at 24-25° had a high lethal temperature of 43.5° C. when subjected to this temperature for 5-10 minutes. No other figures seen for any amphibian exceed 40° C. It should be recognized that in the present instance the tadpoles were brought to temperatures in a very short time, and might have survived greater temperatures had the speed of the rise been slower. On the other hand, they were held at the high temperatures only instantaneously; a longer period at the temperatures cited might have been lethal whereas for a short period it was not. The temperature tolerance of the tadpoles, however, is probably high but perhaps not exceptionally so.

Heat tolerance of adults.—Three adult toads were subjected to conditions similar to those described above. Initial temperatures were 23-24° C., and maximum temperatures were reached in about 15 minutes. As heat was applied the toads showed violent escape reactions, both trying to escape through the cheesecloth cover of the beaker in which they were held and trying to dive through its bottom. Rigor was observed in these animals at temperatures between 39° and 40°. The highest temperature reached on the first run was 41°, which proved fatal. A second toad, brought only to 39.5°, returned to apparently normal activity. Inadvertantly this same toad was used later in a re-run, was brought to a temperature of 40.5°, at which time shock was evident, and then carried on momentarily to 45°. It was removed immediately to cooler water and recovered some ability to move, but was obviously permanently injured.

Two other adults were subjected to high temperatures out of water, in a small bottle with a piece of asbestos furnished for protection (in a trial run without it, the toad apparently died of burns). The bottle was closed with a two-hole stopper with a thermometer in one hole and the other open. This bottle was then suspended in the water bath and the temperature raised. The first showed violent activity, both jumping and attempted digging, up to 42°, above which temperature only weak movements and finally occasional twitches were observed. Throat movements were seen up to 46°, at which time the bottle was removed to cooler water and the temperature rather rapidly decreased to about 25°. Although the toad remained in shock for some time, about three hours later it had returned to a nearly normal posture and rate of breathing and apparently was not permanently injured. The second toad entered shock at about 43°, was brought to only 45°, but did not survive, although treatment was similar to the first. This was a smaller animal, but of course no effects of size difference could be proved from this data.

Again, comparable data are very sparse. Spector's (1956) table 362 indicates that specimens of *Bufo bufo* survived a temperature of 33° C. for one hour (an LD_{50} temperature) in water. Prosser (l.c.) lists high lethal temperatures of 33.5° for *Bufo* and 33° (for one hour) for *Rana*. None of these approach the temperatures tolerated by the present animals, but inadequate information as to experimental conditions make the data difficult properly to compare. It seems likely that the ability of these adult toads to withstand high temperatures either in or out of water may be exceptional among amphibia.

Tolerance to water loss in adults.—Four adult toads were tested for their ability to retain bodily water by confining them to cages of wire and placing them in a desiccator, two over supersaturated solutions and two over dry calcium chloride, for variable periods. The humidity control was far from adequate, since the cages were removed from the desiccator periodically for weight

determinations, but the following results are at least indicative of their tolerances. Weights were determined every hour or half-hour over most of the experiments, which were carried on for period of from ten to 24 hours.

In all four experiments the toads lost water from their bodies at essentially linear rates throughout, until, in one case, death ensued. It is evident that this species has no power to retain body water when away from its aquatic habitat. This agrees well with the conclusion of Thorson and Svihla (1943) that the amphibia have evolved, not a mechanism for preserving bodily water, but the ability to survive extreme losses of that water to the atmosphere.

Three toads, reduced to 72% (in twelve hours over supersaturated zinc chloride), 69% (in ten hours over dry calcium chloride), and 65% (in 24 hours over supersaturated calcium chloride) of their original body weights, recovered to apparently normal conditions after being placed in shallow pans of water. All were able to crawl, although slowly and with difficulty, at the times they were removed from the wire cages. As they were not observed to drink at any time, water replacement is probably through the skin. The fourth toad was carried through until death in a chamber containing dry calcium chloride. Unfortunately, weighings were not sufficiently frequent at the critical period, and only approximate limits may be established. After 17.5 hours the toad was reduced to 62% of its original weight but was still able to move. At 21 hours it was down to 58% and was dead. These figures would appear to bracket the extreme limits of tolerance to water loss. This individual was further completely dried in an oven, with the indication that in the normal condition the body weight is about 77% water.

The water content of the body is in close agreement with similar data for other anurans given by Thorson and Svihla (*l.c.*). Comparison of the tolerance to desiccation with their tables indicates, however, that this species may be less tolerant than other members of its genus, even *B. boreas*, with which it is considered by some to be conspecific. For comparison, the following data are reviewed:

Species	*ave. % loss body wt.*	*ave. % loss body water*
Bufo boreas	44.6	55.8
Bufo terrestris	43.3	54.9
Bufo exsul (this expt.)	40.0	52.0 (approx.)
Hyla regilla	40.0	50.3
Hyla cinerea	39.3	49.0

It is apparent that this toad is fully adapted and restricted to its aquatic and aquatic-border communities. It has been observed some feet from the water, but infrequently, and never at such distances as other toads may often be found in more moist parts of the country. *Bufo exsul* is very dark in color (an adaptation to, if anything, the black mud of its habitat); rapid water loss as evidenced by these experiments may aid it in withstanding the high air temperature of its habitat. Since high temperatures and very low humidities (often less than 10% RH) are quite common in the desert area it inhabits, it is not surprising that the toad is tolerant of both heat and a high degree of water loss. Since any prolonged period away from water would surely prove fatal, and as the distribution of springs in the area is most sporadic, it is further clear why this species might have evolved a greater dependence on water than is characteristic of some of its congeners, from which it is abundantly well isolated geographically, if not taxonomically.

SUMMARY:—Experiments with tadpoles of *Bufo exsul* indicate that heat death ensues between 41° and 42° C. Similar experiments with adults show them to be slightly less tolerant of heat than the tadpoles if confined to water, but able to withstand air temperatures up to 46° C. if evaporation cooling is possible. The adults appear able to survive a loss of water from their bodies equivalent to (approaching) 40%, which amounts to slightly over half of their total water content. These data may be interpreted as adaptive with reference to the occurrence of the toad in isolated springs in a desert valley.

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A MECHANO-GRAPHICAL INSTRUMENT FOR ANALYZING OSCILLOGRAMS

In recent years the use of automatic recording instruments in the biological sciences has greatly increased. In ecological studies it is often very advantageous to use recording instruments. The calibration curves of some of these instruments are non-linear, and some require certain corrections before they can be applied; some have drifting base lines. These corrections and interpretations are time consuming. Such difficulties were encountered in a study of amphibian sounds, in which the output of the electrical analytical system was an oscillographic tracing. Here both linear and non-linear calibration curves were employed for various measurements. In addition, the height of each peak on the oscillogram had to be multiplied by a correction factor before it could be applied to the calibration curve to obtain the analogue value. Early in the project this was done by use of dividers, a scale, and a slide rule. It was soon obvious that some faster method was desirable. The instrument described here was designed to fill these needs; it speeds up the process of analyzing oscillograms by a factor of 20 and increases the accuracy with which measurements may be taken.

The operation of the instrument is based on a graphical interpretation of the equation:

$$f(x) = mx + b,$$

where $f(x)$ is the ordinate, x is the abscissa, m is the slope or tangent value of the curve, and b is the value of

$f(x)$ where the curve intersects the ordinate. If nonlinear calibration curves are used, b must be 0, but when linear calibration curves are used, b may be assigned any value. The instrument can also be used to obtain the ratios of heights of peaks, x_i, for 1 through n on the oscillogram to the height of a given peak, x_0. For this purpose the instrument is adjusted so that it multiplies the height of each peak by a value of m such that $x_0 = 1$, and so that $b = 0$; then the ratios x_i/x_0 will be $f(x_i)/1$. These latter values could then be read from the calibration curve.

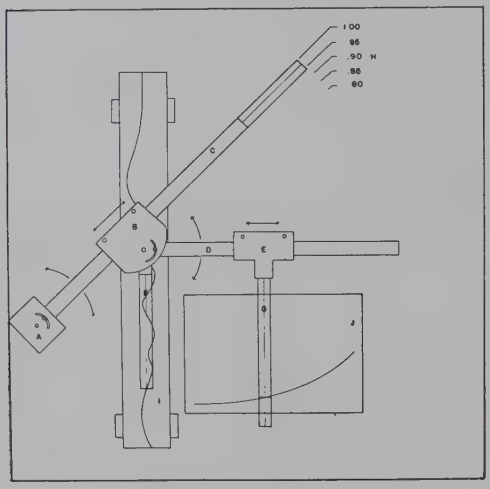

FIG. 1. Mechano-graphical Analyzer. See text for explanation.

Only the basic design and operation will be considered here. There are many modifications possible in its design which would extend its range and simplify its operation. The instrument (see figure) consists of a tangent bar "C" pivoted to block "A" which is fastened to the base board. The bar "D" is pivoted to slide block "B" which slides on the tangent bar. The hairline "G" is fixed to the block "E" which slides on bar "D." The hairline "F" is at a right angle to bar "D" and is parallel to hairline "G." There is an adjustable reference point on hairline "G." The graduations "H" are tangent functions. All calibrations are made in respect to a reference line near the lower edge of the base board.

To make a measurement, one sets the tangent bar to an angle which will give the desired constant multiplier (tangent value), and the bar "D" is set parallel to the reference line. The oscillogram "I" is placed at a right angle to the reference line. The calibration chart "J" is placed so that its base line is under the reference point on hairline "G" when the hairline "F" is on the baseline of the oscillogram. The abscissa of the calibration chart is set parallel to the reference line. The hairline "F" is then moved, by sliding block "B" until it is in line with the peak to be measured. In doing this the height of the peak is multiplied by the constant multiplier. That is, the reference point on hairline "G" is thereby moved to the value of their product. The slide block "E" is then moved so that the reference point on hairline "G" is coincident with a point on the calibration curve. The measurement is then indicated by the hairline "G" on the abscissa of the calibration curve.

The instrument is equally useful with linear and nonlinear curves. The reference point on hairline "G" is movable; this aids in the initial adjustment and allows a constant factor to be added or subtracted when linear curves are used. If the baseline of the oscillogram is displaced, this reference may be moved to correct for the displacement.

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ROLE PLAYED BY DIETARY FAT IN PEROMYSCUS EXPOSED TO LOW TEMPERATURES[1]

It has been shown that if *Peromyscus* are exposed to freezing temperatures without food they will begin to die within a few hours (Sealander 1951). Howard (1951) has pointed out the necessity of a nutritious diet if these rodents are to withstand exposure to low temperatures. In this laboratory it was found that diets such as commercial dog food would not maintain life in individually caged adult *Peromyscus* exposed for long periods to freezing temperatures. However, the addition of peanut butter to the diet would greatly prolong survival under these conditions. This suggests that a diet rich in fat is necessary if these rodents are to survive long periods of such treatment.

With the above in mind, the following experiments were conducted in an effort to more fully evaluate the role played by dietary fat in *Peromyscus maniculatus* exposed to low temperatures. In the first experiment, 24 adult mice weighing 18 to 21 grams that had been live-trapped in the vicinity of Fort Collins, Colorado were divided into two groups of 12 each. Each mouse was placed in an individual cage without nesting material and all of the cages were placed in a walk-in refrigerator maintained at 32° F. The mice in the first group were fed a low fat diet in which 10 percent of the calories consisted of fat, the remaining calories were supplied in the form of dextrins. Those in the second group were fed a similar diet except that 35 percent of the calories were supplied isocalorically for the dextrins in the form of fat. They were equivitaminic and contained all necessary minerals. The ingredients of these two diets are given in Table I. All of the mice were given water *ad lib.* The average daily food consumption per mouse for the mice restricted to the low fat diet was 4.1 grams. For the group restricted to the high fat diet it was 3.9 grams. These differences are not significant. After 45 days of exposure 11 of the 12 mice restricted to the low fat diet had succumbed while only one of the mice restricted to the high fat diet had died.

The above shows the importance of a diet rich in fat

[1] This paper represents a portion of a Ph.D. thesis done under direction of Dr. C. A. Tryon, Jr. at the University of Pittsburgh.

TABLE I. Ingredients of the high and low fat diets.

Ingredient	Low Fat Diet		High Fat Diet	
	Grams	% of Diet	Grams	% of Diet
Casein, crude	4.50	17.25	4.50	19.9
Cornmeal	11.30	43.20	11.30	50.0
Sugar, beet	2.50	9.56	2.50	11.05
Dextran	6.25	23.90	.....	.....
Lard	.66	2.55	3.45	15.25
Salt Mix (No. XIV U.S.P. 1950)	.25	.96	.25	1.1
Sodium chloride	.25	.96	.25	1.1
Yeast, dried brewers	.37	1.42	.37	1.62
Yeast, irridiated	.001	.....	.001	.....
Vit. A concentrate	.001	.....	.001	.....

if these mice are exposed to freezing temperatures in individual cages without nesting material. This experiment does not, however, show whether or not these mice will choose the most beneficent diet as will the white rat (Dugal 1945). Hatfield (1940) has observed that food consumption of *P. maniculatus* increases with decreasing temperature. However, this observation was not with reference to dietary components. It is known that these mice react to low environmental temperatures by building nests of insulating material and huddling together in groups of several animals (Nicholson 1941, Sealander 1952). Therefore, the experiment reported above represents extremely artificial conditions where a single mouse is confined to a cage without nesting material. With this in mind, the following free choice experiment was designed in which it was attempted more closely to simulate conditions found in nature.

Fifteen adult *P. maniculatus* weighing between 18 and 21 grams collected as above were assigned, five each, to three cages supplied with cotton nesting material and wooden shelters. Each cage was supplied with a container of low fat diet and a container of high fat diet and food consumption was recorded. Food not eaten in three days was discarded and fresh food added. Water was also supplied *ad lib.* At the end of the experiment an analysis of variance of the food consumption did not show any significant differences between cages. Therefore, in the following, all of the mice are considered as constituting a single group. Of course, individual food consumption could not be recorded and the reporting of grams of food consumed per mouse per day is followed as a matter of convenience and uniformity. This was obtained by dividing the daily food consumption by the number of mice.

The mice were allowed several weeks in which to adjust and then the cage was placed in a warm room where the temperature was maintained at 85° F. During one month in this warm room the mean low fat consumption per mouse per day was .89 grams; S.D. = .14. The daily fat consumption was .94 grams; S.D. = .13. In terms of percentage, the low fat diet constituted 48.6 percent of the total food consumed, and the high fat diet constituted 51.3 percent of total food consumed.

Following this treatment, the mice were removed to a cooler room and allowed to adjust for one week, then they were placed outdoors and food consumption was recorded for the months of January and February. During this period the mean low fat consumption per mouse per day was .4 gram; S.D. = .19. The high fat consumption during this period was 1.4 grams; S.D. = .22. In terms of percentage, the low fat diet constituted 22 percent of the total food consumption and the high fat diet constituted 78 percent of the total food consumption. The decrease in low fat consumption from the warm room to outdoors is significant $P < .01$. The increase in fat consumption was also significant $P < .01$.

However, the outdoor temperatures during this period, far from being constant, varied from −21.8° F to 66.8° F with the mean temperature of 25.3° F for the entire period. Comparison of the standard deviations of the food consumptions between warm-room and outdoor treatments shows those for outdoors to be nearly twice as large. It was thought that this could be explained by the temperature variations occurring while the mice were exposed outdoors. Therefore, regressions were computed for the mean temperature of each week of the eight weeks of outdoor exposure on the mean high fat consumption of the same periods and also on the low fat consumptions for the same period. In neither case was the regression coefficient significant; therefore the reduction of the sums of squares due to temperature variation was negligible.

These findings show two things. First, unless there is some environmental factor totally overlooked, the significant increase in fat consumption during cold exposure compared to fat consumption during warm exposure suggests that these mice will react to low atmospheric temperatures by choosing a diet rich in dietary fat. Second, the findings from the regressions show that changes in dietary habit do not occur as rapidly as the weather changes in the Rocky Mountain Area. Further proof of this point probably could only be had in a study where the mice were kept in a room where the temperature could be maintained at any desired level for periods of several weeks.

SUMMARY

It was shown that when adult, wild *Peromyscus maniculatus* were confined in individual cages without nesting material a complete diet containing only 10 percent of the calories as fat would not maintain life. On the other hand, a similar diet containing 35 percent of the calories as fat would maintain life.

Similar mice caged together with nesting material were offered both low and high fat diet and were exposed to two consecutive treatments. First, for one month they were exposed in a warm room where the temperature was maintained at 85° F. Second, they were placed outdoors for two months. Outdoors, the average temperature for this period was 25.3° F, ranging from −21.8° to 66° F. Comparison of the food consumption showed that outdoors the mice ate significantly less low fat diet and more high fat diet than they had when exposed to higher temperatures.

The determination of what role, if any, these findings play in these mice under natural conditions will require further investigation.

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FEEDING HABITS OF *MUREX FULVESCENS*

Murex fulvescens Sowerby is the largest member of the family Muricidae in the western Atlantic, attaining a length of 17 centimeters (Clench & Farfante 1945). Because this family also includes the oyster drills or borers *Urosalpinx cinerea, Eupleura caudata,* and *Thais haemastoma* which do great damage to oyster beds along the Atlantic and Gulf coasts, the feeding habits of this large species are of particular interest from a comparative viewpoint.

In July 1957, the collection of eight specimens of *Murex fulvescens* Sowerby from a rock jetty in 1 to 2 meters of water near Beaufort Inlet, North Carolina, provided an opportunity to observe the feeding habits of this gastropod. This paper reports on the numbers and kinds of bivalve prey eaten in the laboratory and the methods employed to open them.

PREDATION IN LABORATORY

On July 13, the eight specimens were placed in a water table two feet square with circulating sea water at the Institute of Fisheries Research. They were maintained in the laboratory for 51 days. During this time, water temperature ranged from 25 to 31° C and salinity, from 34.5 to 36.5 o/oo. The specimens, five males and three females, ranged in length from 10.1 to 13.2 cm.

Several species of bivalves collected near Beaufort Inlet were placed in the water table, and were frequently replaced or renewed during the observational period of 51 days. The following bivalves were consumed by the eight gastropods:

Crassostrea virginica	2.8-17.4 cm.	134
Modiolus demissus	5.5-9.2 cm	33
Mercenaria mercenaria	4.8-8.2 cm	25
Aequipecten irradians	4.3-5.4 cm	6
Ostrea equestris	3.2-5.1 cm	6
Total		204

Of the bivalves presented, *Murex* apparently preferred the eastern edible oyster *Crassostrea*. The fact that *Murex* ate more mussels than clams suggests that the thickness of the clam shell may act as a deterrent to *Murex* predation, as it does to *Busycon* predation (Carriker 1951). Since all scallops were eaten, it is difficult to compare their attractiveness with that of other bivalves.

Ostrea equestris, which seems least attractive to *Murex,* is probably the best represented in the natural habitat of *Murex*. Some edible oysters and an occasional mussel may occur on the jetty rocks where these gastropods were collected, but it is very unlikely that *Murex* would come upon clams or scallops there. Because the availability of these and other species in the natural habitat is unknown (since it is well below the low water mark), it is not clear what role these species play in the diet of *Murex fulvescens*.

The rate of predation obtained in the laboratory was 3.5 bivalves consumed per *Murex* per week, or one bivalve every two days.

METHODS OF PENETRATING BIVALVES

When *Murex fulvescens* attacks *Crassostrea virginica,* it climbs upon the oyster's upper (flat) valve and maneuvers into a position where the outer lip of the aperture rests upon the posterior margins of the valves. By contraction of muscles controlling the foot, a powerful suction is applied, pulling the upper valve away from the lower valve, which is held back by the *Murex* lip. At the first opportunity, the proboscis is extended between the valves, and the rasping of the oyster's soft parts commences. The upper valves of most oysters opened by *Murex* show chipping on the posterior margins where the thinner, more recently secreted shell has flaked off. Occasionally the lower valve also shows chipping where it crumbled under the pressure of the lip. A similar approach serves to open shells of the horse oyster, *Ostrea equestris*.

The actual mechanism of assault upon oysters is the separation of the valves by a powerful pull exerted by the foot. The force required to dislodge a *Murex* from similar attachement to the water table was tested with spring scales. One *Murex* could sustain a pull equivalent to 20 kg before pulling loose, and a second, a pull of 11 kg. All but two could resist a pull of 8 kg without releasing their grip on the bottom of the water table. Crude as these measurements were, they indicate that the foot of *Murex* is a powerful organ which could easily overcome an oyster's adductor muscle. Galtsoff (1952) has shown that a pull of 7 kg exerted upon an oyster's valves is sufficient to cause them to open in less than six hours, and a pull of 10 kg will cause an oyster's valves to open in less than one hour. It is evident that *Murex* is capable of applying the necessary pull.

When *Murex* attacks the clam *Mercenaria mercenaria,* it grasps the ventral margin of the clam in its foot. While the clam's mid-sagittal plane is held perpendicular to the outer lip of the aperture, the end of the clam which extends beyond this edge is drawn inward, into contact with the lip. By repeated contractions of the foot, a grinding action is applied to the end of the valves tangential to their margin. Usually the posterior end of the shell receives this force that scrapes off chips of material. Twelve of 22 clams opened by *Murex* showed chipping at the posterior end of their valves, while seven had been chipped at the anterior end and three, along the ventral margin. When complete closure of the valves is no

longer possible due to the loss of material, *Murex* thrusts its stout muscular proboscis between the valves at the site of chipping and feeds on the soft parts.

An examination of the interior of dry clam shells opened by *Murex* reveals a remarkable halo at the site of entry. It is most pronounced when entry has been effected at the posterior end, for here a whitish zone or streak stands out against the deep purple color normally found in this region of the shell. At the anterior end, this is manifested as a region of whiteness or opacity that contrasts with the relative translucence of adjacent layers of shell. Some of this halo effect may be due to a physical disruption of the shell layers that results from the external chipping; however, miscroscopic examination reveals that most of the halo results from some other cause. Judging from its shape and position, this halo must be attributed to the proboscis of *Murex*.

The halo is not affected by a solution of sodium hypochlorite which would destroy a mucus secretion that had coagulated or dried on the shell. Instead, this halo appears to be a zone of eroded shell produced by a corrosive lubricant from the *Murex* proboscis.

The presence of a yellowish-brown discoloration on two clams immediately adjacent to the chipped margin appears to be additional evidence of a chemical action in the penetration of clams by *Murex*. Until the powerful adductor muscles of *Mercenaria* are cut, the *Murex* proboscis would be squeezed by the valve margins. Secretion of lubricating mucus eases the insertion of the proboscis; if this secretion were capable of eroding sharp edges left by chipping, or of enlarging the narrow orifice, it would give the predator a distinct advantage when penetrating such tightly closing bivalves. There are no shell marks or other indications that *Murex fulvescens* inserts its shell between the two valves for feeding upon *Mercenaria*. Halo formation and chipping were equally developed on both shells—this is in accord with the observation that the chipping force is tangential and is performed by an edge at right angles to the margin of the clam.

When feeding upon *Modiolus demissus*, *Murex* grips the mussel in its foot with the hinged, dorsal edge innermost. The mussel is held with its broad posterior end extending over the outer lip of the aperture, in a position that places its mid-sagittal plane perpendicular to the outer lip. When *Murex* contracts its columellar muscle, drawing the foot inward, the mussel's outer edge is scraped across the lip of the gastropod, grinding bits of material from the *Modiolus* shell. When an opening is formed, the proboscis extends through it and rasps the soft parts. As is the case with *Mercenaria*, the mechanism of attack is actually the grinding of the *Modiolus* shell against the predator's outer lip.

Of 37 *Modiolus* shells opened by *Murex*, all showed signs of chipping. This chipping was always located at the posterior end, and microscopic examination of the margins indicated that the direction of chipping force in every case had been from the dorsal toward the ventral surface. This is probably related to the tendency the mussels exhibited to attach by their byssus to the water table, leaving the dorsal surface exposed. It is surprising that the ventral surface which possesses a byssal opening and which must open for feeding and respiration was not directly approached by attacking *Murex*. Twenty-two shells possessed halos on their interior surface proximal to the site of chipping, similar to, but slightly smaller than the halos found on *Mercenaria* shells opened by *Murex*. Since the *Modiolus* shell is more easily broken and does not close as tightly as that of *Mercenaria*, the *Murex proboscis* is less likely to be pinched while penetrating *Modiolus*. If halo production is attributed to a proboscis which is being squeezed, a smaller proportion of halos among *Modiolus* shells could be expected.

Of the six scallops (*Aquipecten irradians*) opened by *Murex*, three were chipped on their ventro-posterior margin, and one, on its ventro-anterior margin. Two showed no signs of chipping and presumably had been held open by the proboscis, or possibly by part of the *Murex* shell, while feeding took place. Apparently, chipping resulted from intact animals being scraped across the *Murex* lip, the proboscis being thrust through the opening, as was observed for *Modiolus* and *Mercenaria*. However, no *Murex* was observed in the process of attacking a scallop. Since a scallop typically gapes most of the time, it should be much easier for *Murex* to penetrate the valves of *Aequipecten* than those of *Modiolus* or *Mercenaria*.

When a grinding action is applied to the shells of such hard- and solid-shelled species as *Mercenaria*, it would be expected that the outer lip of the *Murex* aperture would suffer similar erosion. The innermost parts of the margin between the spines show signs of wear and sometimes chipping. This was equally apparent on shells of eight specimens which had fed in captivity for seven weeks and on shells of *Murex* in its natural habitat. Many of these worn spots are covered by a layer of new shell which provides a thickened, reinforced lip.

Murex fulvescens exhibits an amazing versatility in the methods of attack employed for different bivalves. The actual mechanism of assault is the grinding of shell margins in the case of the clam and mussel, while in the case of the oyster the valves are pulled apart using the lip as a brace. For feeding, *Murex* holds an oyster with the mid-sagittal plan parallel to its aperture, while it holds a clam or mussel with the mid-sagittal plane perpendicular to its outer lip. The treatment of the latter two species is still different in that the *Murex* foot holds the dorsal surface of a mussel or the ventral surface of a clam. For each species there is a characteristic method of attack, each well suited to the anatomy and habits of that particular species.

The large conchs of the genus *Busycon* also use the outer lip of the shell to open their bivalve prey (Carriker 1951). Similar procedures are used which result in the chipping of margins of clams and other bivalves. However, *Busycon* holds the mid-sagittal plane of its prey parallel to the outer lip of its aperture and chips the margins in this position. The lip functions as a wedge rather than a grinding surface or support as it does for *Murex*. The positional relationships then are quite different, as well as the resultant chipping.

Among the Muricidae, the oyster drills *Urosalpinx* and *Eupleura* open their prey by an entirely different method: by boring a hole into shells with their radula (Carriker 1955). *Thais haemastoma* drills bivalves in a similar manner (Butler 1953). The first report of a gastropod using its shell to open bivalve species is that of François (1891) who studied *Murex fortispina*. (According to Fischer (1922), this is *M. ramosus* L.) This animal possesses a special wedge-shaped tooth which projects inwardly from the outer lip of the aperture. It presses its prey against this special tooth, forcing the valves apart. Only *Murex fortispina* possesses this tooth (Ankel 1938); there is no corresponding prominence in the aperture of *Murex fulvescens*.

Some references to the mechanism of feeding employed by *Murex* (*e.g.* Jensen (1951) and Piéron (1933)) refer instead to *Ocenebra erinacea*, the rough whelk-tingle of

British waters, which was formerly included in the genus *Murex*. It opens bivalves by drilling a hole through the shell with its radula, as does the oyster drill *Urosalpinx* (Orton 1927).

The large size of *Murex fulvescens* makes it unnecessary for this muricid to drill the shells of its prey with its radula. Instead, the corresponding development of a strong columellar muscle enables it to overwhelm bivalves by "brute force." Whether juveniles feed in this manner or drill their prey is unknown.

I wish to thank Dr. Melbourne R. Carriker of the University of North Carolina Department of Zoology for his advice and encouragement during this study.

Summary

During a period of 51 days, 8 *Murex fulvescens* ate 134 *Crassostrea virginica*, 33 *Modiolus demisus*, 25 *Mercenaria mercenaria*, 6 *Aequipecten irradians*, and 6 *Ostrea equestris* under laboratory conditions. The rate of predation was 3.5 bivalves consumed per *Murex* per week. *Murex* opens oysters by pulling the valves apart using the lip as a brace, and clams and mussels by grinding the bivalve shell across the outer lip. A different technique of attack is described for each species. Opaque halos or zones of eroded shell near the site of chipping in *Mercenaria* and *Modiolus* are attributed to material secreted by the *Murex* proboscis which would facilitate entry by the proboscis. The ability to overwhelm bivalves by these means, rather than by radular drilling, is a function of the great size attained by this species.

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REVIEWS

The Study of Lakes[1]

In the beginning of this century, F. A. Forel, investigator of Lake Geneva (Lac Léman) and founder of limnology as a science in its own right, published the first textbook on limnology (Handbuch der Seenkunde. Allgemeine Limnologie. Stuttgart, 1901), a handy pocket-size book. Now, G. Evelyn Hutchinson of Yale University has completed part I of his Treatise on the same subject. Although the biological aspects are to be dealt with in a second volume, this first one on the geography, physics, and chemistry of lakes weighs a good three pounds. The overwhelming difference in size between the textbook of Forel and that of Hutchinson reflects the remarkable increase of facts achieved in the study of lakes during the first half of this century.

Just the richness in facts—several of which are presented here for the first time or collected and digested from sources unavailable to most readers—is an outstanding feature of this new work. In contrast to the practice of many European limnologists, particularly during the inter-war period, Hutchinson does not devote much space to terminological questions but prefers definitions in mathematical form. He has elaborated an extensive system of symbols, covering practically all characteristics of any importance in morphological and physico-chemical descriptions of lakes. If these symbols could be generally accepted and used by limnologists, a considerable step would be taken toward a simpler and more unambiguous presentation of facts.

There are, however, words and concepts beyond the range of symbols and mathematical expressions. What is, for instance, the bearing and scope of limnology? Forel restricted limnology—"the sister of oceanography" as he called it—to the realm of standing waters, principally lakes, and excluded running waters. Hutchinson, though nowhere discussing explicitly the definition of his topic, seems to be of the same opinion and his book deals exclusively with lakes. This is perhaps the only respect wherein Hutchinson is more conservative than contemporary limnologists; most of them include rivers and streamlets as objects of limnological studies, in agreement with Welch (1935) who defined limnology as "that branch of science which deals with biological productivity of inland waters and with all of the causal influences which determine it." According to this point of view a more adequate title of Hutchinson's work would have been "A treatise on lakes." Only a fool could blame the author for not giving such an account of running waters as he has succeeded in giving of lakes, but limnologists studying lotic biotopes may be disappointed not to find their subjects formally treated in this book on limnology.

Students of events occurring in lakes will be all the more delighted. It rarely happens that an author in the first sentence of a preface states that his aim is to give "as complete an account as is possible," and it is still more rare that he is able to do it,—at least for a subject embracing as many aspects as this one of lakes. To penetrate their qualities in *all* respects requires an enormous scholarship with an intimate knowledge of a widely scattered and diversified literature, an unusual ability to combine analytical and synthetical methods and derivations, and personal experience from field and laboratory work on various types of lakes. Finally, to write a textbook where the whole matter is condensed in a useful but still enjoyable form is a task in itself, entailing extraordinary skill and endurance and readily demanding the author himself as sacrifice. The reviewer feels convinced that no one else could write a treatise on lakes as Hutchinson has done. In the face of his "monumentum aere perennius" all criticism is like the cough of a louse on an elephant.

The first chapter, on the origin of lake basins, is the longest (163 pp.) of all seventeen. With a profusion of detailed examples from all parts of the world, the lakes are classified according to the general nature of the processes which have created them. Altogether 76 types are distinguished. Although their "taxonomical" equivalence is sometimes doubtful, they may prove to be helpful in future work. The geologist and geomorphologist will probably appreciate this chapter more than the average limnologist.

Of immediate interest to recent limnology is the second chapter on the morphometry and morphology of lakes. Here, on p. 192 and p. 194, one of the very few errors in the book is found: the level of the Dead Sea is not 980 but 392 m below sea level. Misprints, on the other hand, are not quite so rare but will be easily detected by the observant reader.

After a short chapter on the remarkable properties of water, the hydrological cycle and the water balance of lakes are described. Then follows the hydromechanics of lakes, one of the fields in which the author has made substantial original contributions, but which the biological limnologist may find wearisome to enter, as the author himself points out. Thanks to his clear style, however, the non-mathematical reader, too, should be able to assimilate the chief outlines of water movements, particularly since an excellent summary terminates this as well as all other chapters.

The optical properties of lakes are less well known than are the thermal properties, but both are masterfully treated. A new classification of thermal lake types, based on the frequency of full circulations, is suggested and related to the variations in latitude and altitude, and depth of lake basins. Meromixis and heat budgets are discussed in detail, with use of a good many new data.

The inorganic major ions of rain, lakes, and rivers are presented from new points of view, with the emphasis on the standard composition of ordinary river and lake waters and the deviating compositions in closed basins. Oxygen, the element best known in lake waters, is dealt with in an elaborate manner; but here, as in some other parts of the book, many readers would appreciate if more attention had been paid to the influences of civilization on lakes. Carbon dioxide and hydrogen-ion concentration are discussed on the basis of equations using the most recent constants. The chapter on redox potential and the iron cycle is equally up-to-date. The same holds, to be sure, for the whole book but is perhaps most evident in the excellent chapters on the cycles of phosphorus,

[1] Hutchinson, G. Evelyn. 1957. A treatise on limnology. Volume I. Geography, physics, and chemistry. New York: John Wiley & Sons, Inc. London: Chapman & Hall, Ltd. xiv + 1015 pp., frontispiece + 228 figs., 132 tables. $19.50

sulphur, silica, and nitrogen, and in those on minor metallic elements and organic matter in lake water. Nevertheless, these chapters may be the first to be out-dated because of the present rapid progress in our knowledge of the dynamics of lake metabolism. The introduction of new methods, such as the tracer technique and chromatography, has opened previously unknown perspectives in limnology, too.

A list of symbols, an index of lakes (with geographical bearings), an index of organisms, a general alphabetical index, and a combined bibliography and index of authors containing nearly 1500 references conclude the book. The latter bears witness that the author has considered not only all literature, regardless of language, published into 1956, but also that he is extraordinarily well acquainted with all kinds of papers and reports from the very first beginnings of lake studies on. It is apparent that his encyclopedic knowledge of natural history has been invaluable in the preparation of this book.

All in all, the first volume of Hutchinson's TREATISE ON LIMNOLOGY is a milestone in the progress of lake studies. It will, more than any other book hitherto published, influence and accelerate the future progress in this field. All limnologists and all others interested in lakes certainly look forward to the appearance of the second volume.

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VOYAGE OF THE GALATHEA

Of the four major marine biological expeditions on a world-wide scale ever undertaken, Denmark has been responsible for two. The latest one was the two-year world voyage of the *Galathea*. A volume first published in Danish in 1953 entitled GALATHEAS JORDOMSEJLING 1950-52 (Copenhagen: J. H. Schultz) has been translated into English under the Macmillan imprint.[1] This book gives an account of every phase of the expedition—nautical, mechanical, scientific, and public relations. These various aspects are described by members of the expedition. The scientific accounts range from the major objectives of deep-sea sampling to reports on surface plankton and animal life, sea birds, shallow-water marine communities, freshwater and terrestrial life of islands with indications of the problems of biogeography involved, and ethnology of island natives. Each of the 22 chapters is a separate and complete story in itself, written by 18 specialists. One man wrote three chapters, three men wrote two, 12 prepared one chapter each, and two authors collaborated on one. Some of the chapters of special interest to ecologists are as follows: "Measuring the Productivity of the Sea" by E. S. Nielsen, "Pelagic Fauna" by P. L. Kramp, "Lower Coastal Animals" by Henning Lemche, "Coastal Fish" by J. R. Pfaff, "Animal Life of the Deep Sea Bottom" by A. F. Bruun, "The Density of Animals on the Ocean Floor" by R. Spärck, and "Bacteria in the Deep Sea" by C. E. Zobell and R. Y. Morita.

Some members of the expedition remained with the vessel throughout its world-circling voyage of 63,700 nautical miles. The total scientific staff numbered 38. About 30 of these joined the expedition at various times and places for a limited stretch and for special research studies. These specialists came from nine countries—Denmark, Sweden, India, Indonesia, Siam, Philippines, Australia, New Zealand, and the United States. A shortage of funds unfortunately necessitated a return to home port three months ahead of the original schedule, but not before the primary objectives of the expedition had been accomplished.

This book is a narrative of the voyage and an explanation of the gear, methods, and objectives with a brief summary of some of the accomplishments completed to date, particularly the unique contributions of this expedition. Raw data, descriptions of new genera and species, and technical discussions are not included. Such detailed results will be published elsewhere, and some reports have already been published. Some of the important discoveries, however, are pointed out. Included are the extension of the known depth inhabited by animal life downward some 2.5 kilometers (to a depth of 10,190 meters); extension of the known bathymetric range of many species and groups of marine animals; the quantitative measurement of animal life at great depths which in places proved to be much more dense than expected (e.g. 10 animals per square meter with total weight of 1 gram between 5,000-8,000 meters depth); and proof that bacteria live at the greatest ocean depths. Before the time of this expedition nothing was known about animal life beyond a depth of 6,000 meters. The primary object of this expedition was to explore with the most modern scientific equipment, the major ocean trenches—the Philippine, Sunda, New Britain, Kermadek, and Tonga trenches. In the productivity studies, calculations imply an annual production of organic matter in all oceans of about 40,000 million tons of organic matter, approximately the same as that produced on all land masses. It was also pointed out, however, that "the most productive areas of the sea can produce as much as our best cornfields." A number of new genera and many new species have already been described, and undoubtedly many more will be found new to science when the collections have been thoroughly worked over by specialists. Some of the new animals are illustrated, such as *Galatheathuria* (bathypelagic sea-cucumber), *Lucinoma galatheae* (bivalve), *Antipodocottus galatheae* (bullhead fish), *Galatheathauma axeli* (deep-sea angler-fish); and *Bathycoccus galathea* (barophilic bacteria). No mention is made of the mollusk *Neopilina galatheae* Lemche which represents a group formerly known only as fossil shells and which is now the basis for a new class of Mollusca—the Monoplacophora. The internal segmentation and bilateral symmetry suggest the origin of mollusks from the annelids. Finding this species as a living animal is regarded by malacologists as one of the greatest discoveries of the expedition. Perhaps this discovery was realized too late to include in the present volume although

[1] Bruun, Anton, Sv. Greve, Hakon Mielche, and Ragnar Spärck (editors) 1957. The Galathea Deep Sea Expedition, 1950-1952. Translated from the Danish by Reginald Spink. (Symposium) New York: The Macmillan Co.; London: George Allen & Unwin. 296 pp., 1 map, 221 figs. $8.00.

it has been published elsewhere.[2] Unfortunately no references are given to the original descriptions of any of the new taxa mentioned in the book.

This volume sets the stage for the technical reports which have been and will be published. The text is uniformly well written in spite of the large number of authors; it is well illustrated with diagrams, drawings, and photographs; there is a world map tracing the voyage, a conversion table of measurements, and an index. The only serious lack in the opinion of this reviewer is the total absence of bibliographic references to works already published from this expedition, and plans for future publications are mentioned but once. This one is the projected monograph on "The Natural History of Rennell Island, British Solomon Islands," which will be a joint work with the British Museum expedition.

Ironically, but perhaps expectedly, the inspiration which touched off the spark for this expedition—the elusive sea-serpent—was never found. The book ends with a statement from Dr. Bruun that, "the Great Sea-Serpent has yet to be caught." In spite of this the expedition proved to be eminently successful, and much new knowledge on marine life will be brought to light by the time the final word has been written on the Galathea Deep Sea Expedition.

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[2] Lemche, H. 1957. Nature **179**: 413-416.

THE NEXT HUNDRED YEARS[1]

Geochemist, biologist, and social scientist here address themselves, not to what should happen, but what—in the light of modern knowledge—is possible with respect to world population and resources.

Assuming that the will is present and that humanity does not destroy itself meanwhile, their general judgment is that the Earth can be made to sustain a population of some seven billion for an indefinite length of time. The chief technical problems will be to provide sufficient energy sources, suitable organization, and full use of potential human ability. Clearly and correctly, the authors understand that they are dealing with the interplay of population, resources, and culture.. That the final resolution must be moral and hence cultural is expressed in their final sentence, "the future of industrial society revolves around the question of whether man can learn to live with man."

To this the reviewer is impelled to add, can man learn to live with woman in such fashion that every new child is assured of a welcome and a chance at the good life? The putative figure of seven billion people is a resigned and hopeful bow to the inevitable, even while it tacitly recognizes the biological law that any species must eventually come to terms with the limitations of environment. The authors do not see how such a levelling off can take place at a much lower figure, and indeed suggest that the minimum may substantially exceed it. Their assumption is certainly a reasonable one so long as population policy continues to drift along as it is doing.

Given this postulate, the discussion proceeds in workmanlike fashion to factors of safety. Here there is no suggestion that drift can be tolerated much longer. The operation of the law of diminishing returns with respect to mineral resources is abundantly evident from the chapters dealing with that topic, less obviously so with respect to the production of organic matter and energy. Yet the discerning reader will not find any evidence of hollow optimism.

Thus the feeding of seven billion will require an intensity of production comparable to that of Japan, coupled with a calory intake less than that now available in our country. It will also involve an elimination of the middle term of the plant-animal-man metabolism chain. Adieu to beefsteaks! Access to low-grade mineral sources will require increasing amounts of energy, and this in turn rests upon technological achievements predictable but not yet at hand.

Incidentally, the Japanese are producing 3.2 times the American calory yield per acre at a cost of 3.6 the energy, but with 4.2 times as much human energy expended, and only slightly less supplementary energy. The most intensive food production still requires either heavy input of muscle or a considerable capital expenditure, as our corn and potato champions know well enough. Mechanized farming is not a poor man's game, but it can easily bring poverty to an unskilled manager and ruin to the land.

The authors are quite frank in pointing out that such an increasingly close and elaborate chain of technological operation as they envision becomes ever more vulnerable to breakdown. Even to devise and run it will require, in their opinion, that the system of education and personnel management be driven with a far tighter rein than at present. They are aware, too, of the dangers to personal freedom inherent in increasing social and economic pressures. Likewise they are realistic about the dangers of cultural lag as industrialization progresses, and about the problems of unequal world distribution of raw materials. To their everlasting credit they have no Utopia or fool's paradise to offer us.

In view of the widely held current belief in an ever-expanding economy there is always the danger that this sober and honest book will be read for its promises rather than its warnings. This cannot of course be helped. It does what it set out to do, and does it well. One may regret that any serious discussion of intangible values lay outside its scope. It might well have included some attention to the allocation and use-planning of space, now being heedlessly frozen—often irreversibly so. This, after all, should be a concern of engineers and technologists whose freedom to solve major problems is so often restricted to the immediately urgent.

And perhaps this is an appropriate place to acknowledge our debt to two great Institutes of Technology—Massachusetts and California. The latter is the home base of these authors and of President Dubridge who contributes a thoughtful introduction. Both of these institutes have striven in their research and teaching to broaden the vision of a profession which bears an ever-increasing responsibility in our culture. And both have concerned themselves with fundamentals, with trends and consequences, no less than ingenious expedients.

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[1] Brown, Harrison, James Bonner, and John Weir. 1957. The next hundred years. A discussion prepared for leaders of American industry. New York: Viking Press. ix + 193 pp., 26 figs., 7 tables. $3.95.

Symposium on Populations[1]

This small volume is the report of a symposium held under the auspices of the British Institute of Biology in September, 1954. It includes thirteen short papers by distinguished students of human and animal population problems, each paper followed by a brief report of the discussion of the topic that took place at the time of the conference. This discussion frequently brings out contrasting points of view and serves also to emphasize the essential points that the various authors were trying to make.

The first paper, by A. T. Peacock, deals with economic theory and the concept of an optimum population. Peacock defines the optimum as "that level of population which maximizes real output per head." The difficulties of the concept are amply brought out both in the paper itself and in the discussion. Next, E. Grebenik reviews the growth of human populations, stressing the importance of social rather than biological factors in explaining this growth. I. Schapera in the following paper looks at population growth from an anthropologist's point of view, illustrating the problems of study in non-literate societies with material from the Bechuanaland Protectorate.

J. G. Skellam discusses a variety of mathematical models for different situations in population dynamics. This highly abstract discussion is followed by several papers on animal populations. David Lack, in a paper entitled "The Mortality Factors Affecting Adult Numbers" gives, essentially, a capsule statement of the material in his book on "The Natural Regulation of Animal Numbers," stressing the importance of food limitations. This contrasts with the following paper by Dennis Chitty, entitled "Adverse Effects of Population Density upon the Viability of Later Generations" which stresses other kinds of possible limiting factors. After this comes a paper by Thomas Park reviewing his experimental work on competition between populations of two species of flour beetles, *Tribolium confusum* and *I. castaneum*.

The remaining papers, like the first papers in the volume, focus on man. Leslie Banks writes about "The Relationship between Disease Control and Changes in Population Growth and Age Structure." A. S. Parkes, under the title "Some Biological Aspects of Population Problems," discusses the physiology of conception and research on fertility control. John Hammond reviews what we have learned about the effects of nutrition on fertility in man and in domestic animals. Fraser Darling looks at the special case of pastoral cultures from the point of view of population and resources management. L. S. Penrose briefly surveys the worries of the eugenicists, finding little ground for their concern. Finally, Lord Boyd Orr takes a brave but not too optimistic look at the future of man.

As is inevitable with symposium volumes, this is a series of fragments rather than a balanced covering of the field of knowledge involved. The fragments are, however, remarkably diverse and interesting and thus provide a view of the divergences and complexities of the field of population study that would hardly be possible with a more unified approach. All of the papers have bibliographies so that they serve both as summaries of the opinions of their authors and as introductions to their respective subjects.

[1] Cragg, J. B. and N. W. Pirie (editors). 1955. (U.S. 1957). The numbers of man and animals. (Symposium) Edinburgh: Oliver & Boyd; New York: The Macmillan Co. viii + 152 pp., 13 figs. $2.75.

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Range Management[1]

The relatively young science of range management was born and nurtured in the western United States, one of the most recently settled grazing regions of the world. This science brought to bear newly discovered ecologic principles upon an art as old as history itself. Attention was thereby focused for the first time in history upon the soil and the plant community, and their responses to grazing use, as well as on the grazing animals. Such a revolutionary approach fathered a multitude of publications of the government bulletin and periodical article type. But it was not until 1943 that this amorphous mass of material was brought together and organized, along with much unpublished material, in the first edition of Range Management.

The first edition was an instant success. It was adopted as a text almost universally, and was used as a working reference book by range technicians and practical stockmen throughout the West. And it found its way into the libraries of land administrators throughout the world.

However, in a field which is developing so rapidly, a book soon becomes obsolete. Principles do not change, but they become more fully understood, and particularly in an applied science, new applications are constantly being sought and found. Such changes prompted the publication of the second edition in 1955.

The second edition orients the reader with three chapters which summarize the history of range management, and describe the range as it occurs in the western U. S. today. Basic principles are set forth in chapters 4 to 6, which cover the fields of plant physiology and plant ecology in relation to grazing, and techniques used in range management. Finally, chapters 7 to 16 deal with practical applications of principles to the management problems encountered on the range.

Range inventory methods, which are treated in detail, undoubtedly changed more than any other phase of range management between the dates of the first and second editions. The vegetation "density" concept, originally devised in 1910 and used from then until recently, provided the basis for an empirical method of calculating grazing capacity. From the beginning, there has been considerable dissatisfaction with the method. Several estimated factors were used in the formula to calculate a grazing capacity estimate, which in the end was nothing more than a composite of all the errors in the aforementioned estimates. Worse still, it gave only an indirect

[1] Stoddart, Laurence A., and Arthur D. Smith. 1955. Range management. 2nd edition. New York: McGraw-Hill Book Co. (American Forestry Series.) vii + 433 pp., 156 figs., 69 tables. $7.00.

indication of the effect of past management on the condition of the range vegetation, and the need for changes in management. Chapter 7 brings the reader up to date on various evolutionary approaches to range inventory, and points out the direction of probable future development.

A distinct high point of the book is chapter 11, covering nutrition of animals grazing range forage. In the past, nutritive data have been largely limited to domestic forages. When nutritive values were available for range plants, they more often than not were simple chemical analyses. Particularly with the woody plants of the range, results of chemical analysis may be deceptive. The authors, in their research programs at the Utah Agricultural Experiment Station, have worked out preliminary methods of conducting range digestion trials which provide the most advanced information available concerning the digestibility of range forages for sheep and deer. These methods, and the information resulting from their use, have instituted a new era in range nutrition.

Historically the whole concept of multiple use of wild lands, fundamental to the philosophy of range management, has developed to its ultimate degree in Utah, where the resources of water, timber, forage, wildlife, and recreation are found in an unusually equal balance. The Utah State University College of Forestry, and the authors as members of its staff, have pioneered the development of this philosophy. RANGE MANAGEMENT reflects multiple-use philosophy throughout, and devotes two chapters specifically to its development. Furthermore, the fortunate geographic location of the authors' working center allows them to speak with authority on a surprising number of the practical problems of their field.

A minor criticism could be made of the manner in which grazing regions of the U. S. are handled. While the authors explain that *grazing types* and *vegetation types* are not strictly the same thing, and that *vegetation regions* may include a number of grazing types, they title chapter 3 "Grazing regions of the United States," but then proceed to describe the vegetation regions. Vegetation regions are unsatisfactory as grazing regions because in some instances, such as the Short-Grass vegetation region, they include areas from Texas to Montana where grazing conditions and practices are widely different, while in other cases, i.e., the Pinion-Juniper or the Chaparral vegetation regions, the vegetation region provides only a part of the range forage used by any one ranch outfit during the grazing year, so could hardly be considered a grazing region. Admittedly, a description of vegetation within a grazing region, such as the Intermountain Region, or the Southwest Region, where grazing practices and conditions are fairly uniform, would necessitate repetition of description of vegetation types occurring in more than one grazing region, and would result in other inconsistencies. But in a range management text it seems that where there is a choice between the two approaches, the final decision should be made in favor of the grazing region classification. Furthermore, a more thorough discussion of the livestock management practices of the regions might be expected.

A cursory glance at the first and second editions reveals that the second edition is almost a hundred pages shorter, and contains four fewer chapters. This economy is effected largely by excluding fringe information, and by placing greater emphasis upon fundamental principles.

This book is an outstanding text for use in a range management course, and also is so full of practical information that it is invaluable to land administrators and stockmen. It provides an excellent example of the application of ecologic principles to practical problems of everyday living.

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TWO SYMPOSIA ON DESERT ECOLOGY[1, 2]

The books reviewed here constitute the two latest in a valuable series of symposia which have appeared within the last ten years and which deal with arid land research and problems. Actually, the two volumes are quite different in function, approach, and probable reference value.

The UNESCO book is a collection of ten reports written in 1952 by well-qualified plant ecologists with considerable experience in widely separated arid regions. These reports summarize the results of more than 3,000 research papers, certainly the most comprehensive synthesis yet attempted toward bringing together the scattered and diverse literature on desert and semi-desert plant ecology. As such, it will be a valuable reference work for many years to come for all arid land ecologists. Indeed, it is unfortunate that it is paperbound because physically it is a large volume and the binding will certainly not stand up under the use which it will get. Already, the reviewer's copy is beginning to lose its cover. Considering the excellence of the paper and typography, most users would not mind paying a little more for a more lasting binding.

The ten reviews cover:

Afghanistan, India and Pakistan by F. R. Bharucha

Iran, Israel and Turkey by H. Boyko

Latin America by A. L. Cabrera

Australia by J. Griffiths Davies

Iraq, Jordan, Lebanon, Saudi-Arabia, Syria and Yemen by P. Delbès

Egypt, Eritrea, Libya, and the Sudan by Mohammed Drar

Angola, Southwest Africa, Bechuanaland, and the Union of South Africa by R. Q. Dyer

Northwestern Africa by E. Emberger

United States and Canada by W. G. McGinnies

Tropical East Africa by R. E. Pichi-Sermolli

The book is bilingual: English and French. The papers by Delbès and Emberger are in French with English summaries; all others are in English with French résumés. The index of scientific plant names is a valuable addition.

It is immediately apparent that the extensive arid re-

[1] UNESCO. 1955. Arid zone research—VI. Plant ecology. Reviews of research. (Symposium) Paris: United Nations Educational, Scientific and Cultural Organization. 377 pp., 8 pl., 5 folded maps. Paperbound: $7.00.

[2] White, Gilbert F. (editor). 1956. The future of arid lands. (Symposium) Washington: American Association for the Advancement of Science. Pub. No. 43. 453 pp., 49 figs. $6.75.

gions of the U.S.S.R. and China are not covered. This leaves an unfortunate, but unavoidable, gap in this otherwise comprehensive series of reports. It is to be hoped that the future will see material on this Eurasian region made available to all ecologists.

In general, the reviews are excellent. The literature lists alone are worth the cost. As background reference sources, these papers are invaluable to any current or future research in dry land ecology. In the opinion of the reviewer, all ecologists interested in arid regions will need this book.

The Future of Arid Lands is the collection of papers and the recommendations from the International Arid Lands meeting held in New Mexico (Albuquerque and Socorro) in 1955 and sponsored by the AAAS. Unlike so many symposia in which there are only loosely related articles, this symposium is relatively tightly woven and asks some rather pointed and definite questions on the future of dry regions. The various papers, in general, speak to the points of these questions; and attempts are made to summarize the answers.

The symposium was divided into five parts:

1. The broad view
2. Variability and predictability of water supply
3. Better use of present resources
4. Prospects for additional water sources
5. Better adaptation of plants and animals to arid conditions

Distributed through these divisions is a total of 34 papers.

As is to be expected in such a large symposium, the papers vary widely in quality and there is considerable repetition. Nevertheless, there are some solid contributions, notably in the papers by Tixeront on "Water resources in arid regions," by Wallén on "Fluctuations and variability in Mexican rainfall," by Schaefer on "Some relationships of experimental meteorology to arid land water sources," by Love on "Better adaptation of plants to arid conditions," and by Schmidt-Nielsen on "Animals and arid conditions: physiological aspects of productivity and management."

In general, the subject matter papers seem better than the general papers with the exception among the latter of the excellent ecological introduction to the symposium by H. L. Shantz. Since the problems of arid land use are primarily ecological, one would suppose that the whole symposium could also have been summarized in terms of the functioning of arid land ecosystems with the limiting factors under control. Very little attention has been given to a synthesis of recommendations in terms of modern ecosystem ecology. Nevertheless, is is refreshing to find in Love's article some criticism of the long-held, but fallacious, idea that climax vegetation (as opposed to successional stages) is most productive in terms of removable crops.

To the reviewer, the best section appeared to be that on prospects for additional water sources. Koenig's paper on the economics of water sources at the end of this section brings scientific theory down to practicality with some eye-opening figures concerning the costs of increasing water use in climates with high evaporation rates. His conclusion: agriculture with its high water need may not be as efficient a use of these regions as would be provided by some types of industry in these days of relatively abundant transportation.

Naturally, there is a preoccupation throughout the symposium with water as the limiting factor. More attention could have been paid to the local, but important, limiting factors of temperature and soil parent materials. These have a great effect on the distribution of native plant species in the desert and upon subsequent agricultural use, and their effects are not so easily counteracted.

The book was meant to be, and is, a contribution toward solving *practical* problems connected with the increased use of arid lands. As such, the list of recommendations of the conference should be heeded by all concerned. The dry regions constitute one of the last frontiers of opportunity in land use, and let us hope that they will be used more wisely in the future than they have been in the past. Symposia such as this will do much to guide such use in the right direction. In the words of Gilbert F. White, the symposium editor, ". . . the Symposium was a point of departure rather than a summing up, and in this sense the future of arid lands is in some part shaped by those who sought to assess its prospect in 1955."

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Rain Forests of Golfo Dulce[1]

The title of this magnificently produced book on the forests of the Pacific Coast of southern Costa Rica leads one to expect an ecological work, but in fact its interest is almost entirely floristic. The last 300 pages of the book are devoted to an "Alphabetical Index to the Families, Genera, Species and Common Names," a treatment which falls somewhere in between that of a conventional flora and the check-lists of trees and shrubs often issued by Forestry Departments. Genera are keyed if there is more than one in a family, and species likewise; there is no synonymy given but specimens are cited. Descriptions are confined to the most obvious and easily recognizable characters, as is usual in check-lists. There are 21 excellent line-drawings of specimens and 123 equally excellent photographs, again mainly of specimens but occasionally of the whole plant or of its roots or fruit. Publication of 10 new species is included. Only trees and shrubs are listed which, as the author tells us in the introduction, means a selection of 72 families, 267 genera and 433 species out of a total of 134 families with 662 genera and 1315 species for which records exist for the area. A better title for the book would have been "Trees and Shrubs of Golfo Dulce."

In the earlier part of the book 30 pages are devoted to other forms of species lists; plants with conspicuous flowers are keyed, then species with conspicuous vegetative characters, species which harbour stinging ants, and species which occur in concentrated stands. This is followed by utilisation lists. The second chapter, pp. 7 to 85, is headed Ecology but turns out to be only a heading for different kinds of species lists. Under each ecological category (of which there are thirteen) there are one or more paragraphs giving brief details of the habitat and

[1] Allen, Paul H. 1956. The rain forests of Golfo Dulce. Gainesville: University of Florida Press. xi + 417 pp., 22 figs., 34 plates, and taxonomic keys. $8.50.

structure, followed by species lists, by strata where present, and then various keys to these species ingeniously constructed entirely upon the most obvious vegetative characters without recourse to floral analysis. For practical use in tropical forests this is of course the ideal approach and is no new thing in tropical forestry.

The ecological units are divided into climatic, edaphic and transitional formations, the last-named being modified by human intervention. The climatic formations include the following:

Evergreen Lowland Forest, on reasonably well-drained river flood plains, with a rainfall of 140 to 200 inches. There is for the most part a well-marked dry season and both in structure and flora the forests have a well-marked seasonal character. No associations are recognized.

Littoral Woodland, normal for tropical America.

Lower Montaine Rain Forest, on mountain and hill slopes up to 2,500 feet, evidently embraces a variety of types as twelve associations are recognized, some of which must differ rather widely. The flora of this formation suggests that it is not perhaps truly montane in character but may be found to consist of lowland associations of a semi-evergreen or dry evergreen type.

Upper Montaine Rain Forest, above 2,500 ft., comprises a variety of montane types including palm stands, but it seems that the designation "upper montane" implies an exaggeration and is unwarranted. Six associations are recognized.

Edaphic formations include *Swamp Forest* and *Palm Swamp*; freshwater swamps of Pterocarpus and Symphonia with Carapa and Mora, and the palms Raphia, Corozo and Scheelea.

Mangrove Woodland presents the usual Rhizophora, Avicennia and other species, and *Herbaceous Swamp* too gives us familiar Paspalum, Cyperus, Heliconia, etc. A category of *Gallery Woodland* is included to deal with the arborescent species peculiar to river banks and gravel bars: five associations are recognized.

Transitional formations include first *Savanna* which the author considers probably to have resulted from clearing and burning of the forest. *Curatella americana* and *Byrsonima crassifolia* are typically present. "It is believed that trees would gradually reinvade the savanna if fires were controlled." If only someone would put this theory to the test, at the same time trying to create savanna by felling and burning forest, much controversy might be resolved. Under *Pastures* the casual trees which continue to survive in pastoral areas are listed, while *Fence Rows and Trailside Thickets* and *Second Growth* are similarly self explanatory.

This book is a truly magnificent floristic work, but does not greatly advance our knowledge of ecology in the area.

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Ecology of Alpine Fungi[1]

Preliminary chapters of this monograph sketch the location and geology of the Swiss National Park. They also describe the alpine zone and its climate. A descriptive catalogue illustrated with line drawings and colored figures of the fungi precedes the ecological considerations.

The most important contribution of this work is that it demonstrates how the mycologist can aid the ecologist in describing plant associations. The alpine zone of the Swiss National Park contains no previously recognized forest community. There are meadows, marshes or bogs, barrens, rock outcroppings, alpine prairies, and local to extensive patches of woody plant communities composed of *Loiseleuria* and especially of *Dryas octopetala* and four species of dwarf *Salix* belonging to the section *Glaciales*. Since *Loiseleuria* is an ericad its mycorrhizae are endotrophic and thus are not related to the Hymenomycetes.

Associated with the *Dryas* and *Salix* species, however, are a large number of species of macrofungi usually found only in the forest. Most known species in the genera concerned, especially in *Inocybe* and *Cortinarius*, form ectotrophic mycorrhizae with forest trees. Since *Dryas* and *Salix* roots in the alpine zone have been shown to possess ectotrophic mycorrhizae, it is assumed that this type of relationship exists between the common fungi of these woodlands and their woody associates. Because of this relationship the *Dryas* and *Salix* pigmy forests are set aside in a special alpine zone Association, the Microsylve. As demonstrated by constancy of occurrence, this association is considered a valid extension of the description of the alpine flora.

The problem of nanism in alpine fungus fruit bodies is important. In meadow, prairie, marsh, and coprophilous fungi nanism is demonstrated, if at all, by a dwarfing of the pileus and stipe. The fungi of the microsylve also show smaller size than the same species in the forests of the lower slopes, but this is more marked. It is suggested that because of decreased food supplies as a result of mycorrhizal association with pigmy trees, the nanism is easily explained.

Several characteristics of the fungal fruit bodies are affected by nanism. The stipe becomes shorter and usually stouter, the pileus has a smaller diameter and may be plane rather than convex at maturity, and the lamellae become fewer in number but broader. In addition, the base of the stipe becomes grooved, few species occur in clusters which are composed of only a few individuals, and more species possess veils. Spores of 64 species belonging to all groups of fungi have been measured in comparison with spores of the same species found at lower elevations. Of these, 47 showed no differences in length or breadth, 16 species had larger spores, and one had smaller. Size differences found were considered only of relative value, not genetically distinct variations.

It was found that while the highest extension of the sylvatic zone from the lower slopes reached 2250-2300 m, at least three fungi reached above 2800 m. Twenty-five species were found between 2700 and 2800 m.

Within the Alpine Zone 202 species of macrofungi were found in the Swiss National Park. Of these, 115 species or 57% are ubiquitous in contrast with 7.4% of the 420 species of flowering plants. It is suggested that more than 40 of the species associated with the the microsylve extend beyond the alpine regions of Europe to the Arctic where they may be associated with the same mycorrhizal hosts over a very broad territory. From their known distribution, other species extend beyond the alpine re-

[1] Favre, Jules, 1955. Les champignons supérieurs de la zone alpine du Parc National Suisse. (The higher fungi of the Swiss National Park) Résultats des recherches scientifiques enterprises au Parc National Suisse. Part 5, new series, 33: 1-212. 145 text figures, 11 plates (8 in color). $7.00.

gions of Europe to Scandinavia, Lappland, Iceland, Spitzbergen, Greenland and lands within the Arctic Circle. A few species extend into montane North and South America. Since the fleshy fungi of the Arctic have never been studied extensively or intensively, it is not presently possible to correlate the distribution patterns of arctic and alpine fungi.

Studies such as this can extend our knowledge of plant distribution and our understanding of geographic botany, and may be able to help explain anomalies of floristic discontinuities.

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Japanese Publications in the Field of Ecology

This review is to offer, at the suggestion of the review editor, some information on Japanese publication in the field of ecology since the war. European ecology, primarily in the form of German natural history, was introduced into our country toward the end of the 19th century by the late Professor M. Miyoshi of Tokyo University; and thereafter ecological conceptions from northern and middle Europe, England, and America were brought into Japanese work one after another. Because research workers and chairs of ecology in Japanese institutions were few, ecological studies were not vigorously pursued in former times. Since the war, however, interest in ecology has greatly increased; training and research in the field have been, to use an American expression, booming. In this, Dr. K. Imanishi of Kyoto University has been a major influence; in 1948 he published his monumental book, "The logic of biotic societies." (I also published the book, "A criticism of modern biology," discussing the character of modern ecology, in 1948.) Since that time, several books have been written and published, as listed below, and Japanese translations of the well-known books by Elton and Odum have appeared.

The expansion of ecological interest since the war is reflected also in the membership of the Japanese Society of Ecology, which has now more than 1000 members. This Society was founded in 1953 after the consultation of three bodies, the Plant Ecological Society (Prof. Y. Yoshii), the Round-Table Conference of Animal Ecology (Prof. D. Miyadi), and the Phytoecological Society of Japan (Prof. M. Monshi), and has had Prof. Y. Yoshii, now at Gifu University, as its president since its establishment. American ecology has been an important influence on the growth of the Society. American and other foreign ecological studies are freely available to Japanese ecologists; but the movement of ecological findings from Japanese into foreign publications has not been so free. Our difficult language has no doubt been a major reason the exchange of ecological knowledge has been somewhat one-sided, and some Japanese work of interest has been largely unnoticed abroad. Motomura's (1932) law of geometrical progression, for example, was closely related to Fisher and Williams' logarithmic series and Preston's lognormal theory on relative numbers of individuals in species, and preceded by some years these British and American developments. In the hope that it may be helpful or of interest to American ecologists, and that the considerable extent of present Japanese ecological research and publication may be better appreciated, I shall offer here an outline of publications of three groups: first, Japanese journals largely concerned with the field of ecology; second, other Japanese journals in which ecological papers often appear; and third, Japanese books on ecology.

I. Japanese ecological journals

1) Ecological Review (1935-1949, 12 vols.) This is the oldest Japanese journal of ecology, as such, edited by Y. Yoshii and published quarterly by the Hakkoda Botanical Laboratory, Tohoku University, Sendai, with original papers and abstracts in Japanese. Since the 13th volume this has been issued as a closed journal from the Hakkoda Botanical Laboratory.

2) Bulletin of the Society of Plant Ecology (1951-1954, 3 vols.), which succeeded Ecol. Rev. and was also edited by Y. Yoshii, for the Plant Ecological Society, Tohoku University. It contains original papers in Japanese with English summaries, and abstracts in Japanese.

3) Japanese Journal of Ecology (1954-, 7 vols. to date). This quarterly journal is the only official publication of the Ecological Society of Japan, c/o Biological Institute, Tohoku University, edited for the Society by M. Kato. It contains original papers from Japanese work, and a few abstracts and notes, covering wide fields of applied as well as basic plant and animal ecology. Articles are usually in Japanese with summaries in European languages.

4) Annals of Phytoecology (1941-1943, 3 vols.), a biannual journal published by the Phytoecological Society of Japan, Tokyo University, edited by H. Nakano, with papers, reviews, and abstracts in Japanese.

5) Physiology and Ecology (1949-, 7 vols. to date), edited by D. Miyadi et al. and published quarterly by the Physiology and Ecology Publishing Association, Kyoto, with original papers in Japanese with English summaries.

6) Insect Ecology (Seitai Konchu) (1946-, 6 vols. to date), a unique journal in its field, published three times a year by Rikusuisha (representative: T. Sugi), 4-112, Iriarai, Ota-ku, Tokyo. It contains original papers, usually in Japanese with European summaries, and notes and abstracts on ecology, life-history, and distribution of insects.

7) Researches on Population Ecology (1952-, 3 vols. to date), a very distinctive ecological publication, edited by S. Utida of Kyoto University and containing original papers on the ecology of animals (mainly insects) written in Japanese, with English summaries.

8) Japanese Journal of Limnology (1931-, 19 vols. to date), edited by M. Ueno for the Japanese Limnological Society, with papers and abstracts in Japanese, with English summaries.

9) Contributions to Physiology and Ecology, Kyoto University (1944-, 80 nos. to date), edited by D. Miyadi for the University of Kyoto, Seto Marine Biological Laboratory, and Otsu Lake Biological Laboratory, and containing longer papers in Japanese, sometimes with English summaries.

II. The following are some—but by no means all—of the Japanese journals which contain fairly frequent papers on

ecology, with numbers of volumes to date and societies or places of publication

1. Hokuriku Journal of Botany, 6 vols., Kanazawa University
2. Acta Phytotaxonomica et Geobotanica, 17 vols., Phytogeographical Society, Kyoto University
3. Oyo-Kontyu ("Applied Entomology" in Japanese), 12 vols., to 1956,
4. Japanese Journal of Applied Zoology, 21 vols., to 1956, and
5. Japanese Journal of Applied Entomology and Zoology, 1 vol. to date, National Institute of Agricultural Sciences, Tokyo
6. Biological Science [Tokyo], 9 vols., Section of Biology, Democratic Scientists' Society in Japan, c/o Laboratory of Botany, Tokyo University
7. Hikobia—Journal of the Hiroshima Botanical Club, 1 vol.
8. Primates—Journal of Primatology, 1 vol., Japan Monkey Center, Inuyama City, Aichi Prefecture
9. The Annual of Animal Psychology, 7 vols., Japanese Society for Animal Psychology
10. Mushi ("Insect" in Japanese), 30 vols., Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka
11. Journal of the Japanese Forestry Society, 22 vols.
12. Bulletin of the Japanese Society of Scientific Fisheries, 22 vols.
13. The Botanical Magazine [Tokyo], 70 vols., Botanical Society of Japan, Tokyo University
14. Japanese Journal of Botany, 15 vols., Science Council of Japan
15. Japanese Journal of Zoology, 12 vols., Science Council of Japan
16. Dobutsugaku Zasshi (Zoological Magazine), 66 vols., Zoological Society of Japan, Tokyo University
17. Annotationes Zoologicae Japonenses, 39 vols., Zoological Society of Japan
18. Journals of various universities— Memoirs of the College of Science, Kyoto University, Science Reports of the Tohoku University, Memoirs of the Faculty of Science, Kyushu University, Journal of the Institute of Polytechnics, Osaka City University, Bulletin of the Tokyo University Forests, etc.
19. Reports of the various research institutions—Bulletin of the National Institute of Agricultural Sciences, Bulletin of the Forest Experiment Station, Miscellaneous Reports of the Research Institute for Natural Resources, etc.

III. Ecological books published since 1950 are as follows:

Ashida, Joji et al., editors. 1958. Organisms and their environment. Tokyo: Kyoritsu Publ. Co. (Modern Biology Series, Vol. 5). 397 pp., 183 figs. and 77 tables. 580 yen.

Elton, C. S. 1927. Animal ecology. Transl. by Toshio Shibuya. 1955. Tokyo: Kagaku-Shinkosha. 450 yen.

Emerson, A. E. 1949. Ecology and evolution (*in* Principles of animal ecology, by W. C. Allee et al.). Transl. by Yoshiaki Ito. 1955. Tokyo: Misuzu-Shobo. 350 yen.

Imanishi, Kinji. 1951. Pre-human societies. Tokyo: Iwanami Publ. Co. 175 pp. and 9 figs. 100 yen.

Kato, Mutsuo. 1955. Experimental methods of animal ecology. Tokyo: Nakayama Publ. Co. (Experimental Methods in Biology Series). 77 pp. and 45 figs.

Kitazawa, Yuzo. 1955. Research methods of ecosystem. Tokyo: Nakayama Publ. Co. (Experimental Methods in Biology Series.) 92 pp., 26 figs., and 27 tables.

Miyadi, Denzaburo and Shuichi Mori. 1933. Ecology of animals. Tokyo: Iwanami Publ. Co. 221 pp., 68 figs. and 24 tables. 250 yen.

Numata, Makoto. 1953. Methodology of ecology. Tokyo: Kokon-Shoin. 254 pp., 20 pp. of references and 22 pp. of glossary. 220 yen.

Numata, Makoto. 1957. Ecology (Experimental Course on Biology, vol. 1). Tokyo: Iwasaki Publ. Co. 125 pp., 78 figs., and 31 tables. 200 yen.

Numata, Makoto. 1958. Standpoint of ecology. Tokyo: Kokon-Shoin. 245 pp., 50 figs. and 18 tables. 220 yen.

Odum, E. P. 1953. Fundamentals of ecology. Transl. by Ecology Research Group, Kyoto Univ. Tokyo: Asakura Publ. Co. 800 yen.

Shibuya, Toshio. 1956. Problems on ecology. Tokyo: Rironsha. 255 pp., 19 figs. and 1 table. 280 yen.

Suzuki, Tokio. 1952. The forest climaxes of East Asia. Tokyo: Kokon-Shoin. 137 pp. and 22 figs. 150 yen.

Suzuki, Tokio. 1954. Methods of ecological survey. Tokyo: Kokon-Shoin. 155 pp., 19 figs. and 9 tables. 180 yen.

Yagi, Nobumasa and Ken'ichi Nomura, editors. 1952. Introduction to ecology. Tokyo: Yokendo. 300 pp., 49 figs. and 26 tables. 300 yen.

Yoshii, Yoshitsugu. 1955. Experimental methods of plant ecology. Tokyo: Nakayama Publ. Co. (Experimental Methods in Biology Series.) 90 pp. and 33 figs.

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A New Journal of Vegetation Mapping[1]

The use of modern, intensive vegetation mapping in Europe has produced a large number of maps and many publications, representing authors and schools of diverse approaches to vegetation and its mapping. A major center of activity in Germany has been the *Bundesanstalt für Vegetationskartierung* at Stolzenau/Weser under the direction of Reinhold Tüxen, from which have originated many papers in the valuable series, Angewandte Pflanzensoziologie [Stolzenau/Weser] and Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft, N. F. [Stolzenau/Weser]. From France, the review editor has received issues of a new Bulletin of the center for vegetation mapping at Montpellier.

The *Service de la Carte des Groupements Végétaux* is

[1] Bulletin du Service de la Carte Phytogéographique (Centre National de la Recherche Scientifique, Série B. Carte des Groupements Végétaux au 20000e). 1956—. Edited by L. Emberger, director, and G. Long, technical director, of the Service de la Carte des Groupements Végétaux. Published by the Centre National de la Recherche Scientifique, 13 Quai Anatole France, Paris-7, France, at present available on request from the Service de la Carte des Groupements Végétaux, Institut Botanique, Montpellier, France.

located at the Institut Botanique de Montpellier, under the direction of L. Emberger; and the new bulletin is edited by Emberger and G. Long. Publication of the journal began in 1956, with a single number of the first volume, and has continued through two numbers of vol. 2 in 1957 to the current issues. Since 1957, each issue includes three parts—original articles, bibliographic analysis, and news. The original articles deal with theoretical and experimental phytosociology, and the application of phytosociology to problems of method in vegetation mapping; in general the BULLETIN is not to publish detailed monographs on local vegetation. The "Analyses bibliographiques" may become a section of interest and value, for it consists of reviews of books and papers of significance in both basic and applied phytosociology. The "Nouvelles" apparently is to include information on current activity relating to vegetation mapping in France and French Africa.

The Service de la Carte des Groupements Végétaux, of the Centre National de la Recherche Scientifique, has been in existence since 1947, with the principal objective of making phytosociologic and ecological studies leading to better knowledge of natural environments and vegetation, especially through techniques of vegetation mapping. Extensive work has been based on large-scale maps 1/20,000, 1/10,000, 1/500 and above) intended to aid in description of environments and rational planning in landscape use, in studies in Tunisia, Morocco, Algeria, and the Near East, as well as France itself. Although Prof. Emberger has been associated with the "School of Braun-Blanquet," there is no formal relation between the Institut Botanique, the Service, and its BULLETIN on the one hand, and the Station Internationale de Gébotonique Méditerranéenne et Alpine, under the direction of Dr. Braun-Blanquet at Montpellier on the other. Papers in the journal include short reviews of techniques—such as the association matrix or Kulczyński triangle approach to sample grouping, and the American 3-step method—which are not part of the usual approach of the school of Braun-Blanquet.

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BOOKS AND MONOGRAPHS RECEIVED FOR REVIEW

Aichinger, Erwin. 1956. Die *Calluna*-Heiden (Callunetum vulgaris) und die *Erica carnea*-Heiden (Ericetum carneae). Angewandte Pflanzensoziologie [Wien] **12**: 1-128, 3 figs. $2.40. Vienna: Springer-Verlag.

Aichinger, Erwin. 1957. Die Zwergstrauchheiden als Vegetationsentwicklungstypen (Fortsetzung). Angewandte Pflanzensoziologie [Wien] **13**: 1-84. $1.55.

Aichinger, Erwin, 1957. Die Zwergstrauchheiden als Vegetationsentwicklungstypen. (Fortsetzung und Schluss). Angewandte Pflanzensoziologie [Wien] **14**: 1-175, 6 figs. $3.55.

Baker, Ralph C. 1957. Fur seals of the Pribilof Islands. U. S. Dept. of Interior, Fish and Wildlife Service, Conservation in Action No. **12**: 1-23, figs. and photos. $0.20.

Behle, William H. 1958. The bird life of Great Salt Lake. Salt Lake City: University of Utah Press. xiii + 203 pp., 43 figs. $4.50.

Bharucha, F. R. & G. Y. Shanbhag. 1957. Precipitation effectiveness in relation to the vegetation of India, Pakistan and Burma. University of Bombay Botanical Memoirs No. **3**: 1-109, 7 figs., 12 tables. Rs. 1.50.

Black, C. A. 1957. Soil-plant relationships. New York: John Wiley & Sons; London: Chapman & Hall, Ltd. vi + 332 pp., figs. & tables.

Blair, W. Frank, Albert P. Blair, Pierce Brodkorb, Fred R. Cagle, & George A. Moore. 1957. Vertebrates of the United States. New York: McGraw-Hill Book Co. ix + 819 pp., 444 figs., keys and glossary. $12.00.

Bold, Harold C. 1957. Morphology of plants. New York: Harper & Brothers. xxiii + 669 pp., num. figs. $8.00.

Braun-Blanquet, J., with collaboration of **N. Roussine** & **R. Nègre,** preface by **L. Emberger.** (1953.) Les groupements végétaux de la France méditerranéenne. Montpellier: Centre National de la Recherche Scientifique (Service de la Carte des Groupements Végétaux) et Direction de la Carte des Groupements Végétaux de l'Afrique du Nord. 297 pp., 16 photos., 3 tables.

Canella, Mario F. 1957. Studi e recerche sui Tentaculiferi nel quadro della biologia generale. (French, Engl., & Germ. summs.: Studies and researches on Tentaculifera (Suctoria) within the frame of general biology). Annali dell'Università di Ferrara (Nuova Serie) Sezione III—Biologia Animale—Vol. **1**, N. **4**, pp. 259-716, 24 figs. & 97 microphotos.

Cloudsley-Thompson, J. L. 1958. Spiders, scorpions, centipedes and mites. The ecology and natural history of woodlice, "myriapods" and arachnids. New York and London: Pergamon Press. xiv + 228 pp., 40 figs. $9.00.

Collins, Stephen. 1956. The biotic communities of Greenbrook Sanctuary. Englewood, N. J. (Box 230): Palisades Nature Association. v + 112 pp., 82 figs., topog. & vegetation maps. $2.50.

Critchfield, William B. 1957. Geographic variation in *Pinus contorta*. Maria Moors Cabot Foundation Publ. No. **3**, vii + 118 pp., 26 figs., 10 tables. Cambridge, Mass.: Harvard Univ.

Curry-Lindahl, Kai. 1957. Fiskarna i färg. [Fishes in color.] 3rd ed. Stockholm: Almqvist & Wiksell. viii + 189 pp., 64 color plates. 11:- kr.

Cutler, E. J. B. 1957. Soils of the Lower Clutha Plains. New Zealand Dept. of Scientific and Industrial Research, Soil Bureau, Bull. **15**: 1-40, 13 figs., soils map. 12s. 6d.

Dales, R. Phillips. 1957. Pelagic Polychaetes of the Pacific Ocean. Bulletin of the Scripps Institution of Oceanography **7**(2): 99-168, 64 figs. $3.00. Berkeley & Los Angeles: Univ. California Press.

Druce, A. P. 1957. Botanical survey of an experimental catchment, Taita, New Zealand. New Zealand Dept. of Scientific and Industrial Research, Bull. **124**: 1-81, 15 figs., 11 tables, 4 maps. 15/-

Drury, William H., Jr. 1956. Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska. Contributions from the Gray Her-

barium of Harvard University, No. **178**: 1-130, 24 figs.

Errington, Paul L. 1957. Of men and marshes. New York: Macmillan Co. ix + 150 pp., figs. $4.50.

Galoux, A. 1953. La Chênaie sessiliflore de Haute Campine. Essai de biosociologie. Travaux de Station de Recherches de Groenendaal, Série A, No. **8**, 235 pp., 44 figs., 45 tables.

Garman, E. H. 1957. The occurrence of spruce in the interior of British Columbia. British Columbia Forest Service Technical Publ. **T. 49**: 1-31, 5 figs., 6 tables. $0.50.

Goodlet, John C. 1954. Vegetation adjacent to the border of the Wisconsin drift in Potter County, Pennsylvania. Petersham, Mass.: Harvard Forest Bull. No. **25**: 1-93, 15 figs., 6 plates. $0.50.

Greig-Smith, P. 1957. Quantitative plant ecology. New York: Academic Press, Inc.; London: Butterworths Scientific Publications. ix + 198 pp., 29 figs., 27 tables.

Guthrie, Mary J. & John M. Anderson. 1957. General zoology. New York: John Wiley & Sons; London: Chapman & Hall. xv + 708 pp., num. figs. $7.50.

Hatch, Melville H. with collaboration of **M. W. Sanderson & G. A. Marsh.** 1957. The beetles of the Pacific Northwest. Part II: Staphyliniformia. Seattle: University of Washington Press, Univ. Wash. Publ. in Biology Vol. 16. ix + 384 pp., figs. & taxonomic keys. $7.00.

Hedgpeth, Joel W., editor. 1957. Treatise on marine ecology and paleoecology. Vol. 1. Ecology. (Symposium) New York: Geological Society of America Memoir **67**. viii + 1296 pp., figs. $12.50.

Hickman, Cleveland P. 1956. A field manual of animal ecology and natural history. Minneapolis: Burgess Publishing Co. v + 125 pp.

Hoffmeister, Donald F. & Carl O. Mohr. 1957. Fieldbook of Illinois mammals. Urbana: Illinois Natural History Survey Manual **4**, xi + 233 pp., 119 figs. $1.75.

Klapp, Ernst. 1956. Wiesen und Weiden. Behandlung, Verbesserung und Nutzung von Grünlandflächen. 3rd ed. Berlin and Hamburg: Paul Parey. vii + 519 pp., 175 figs., num. tables. DM 33,60.

Klapp, Ernst. 1957. Futterbau und Grünlandnutzung. Ein Wegeiser für die Praxis. 6th ed. Berlin and Hamburg: Paul Parey. 167 pp., 51 figs. DM 8,40

Klapp, Ernst. 1957. Taschenbuch der Gräser. Erkennung und Bestimmung, Standort und Vergesellschaftung, Bewertung und Verwendung. 8th ed. Berlin and Hamburg: Paul Parey. 220 pp., 750 figs, taxonomic keys. DM 9,80.

Larimore, R. Weldon. 1957. Ecological life history of the warmouth (Centrarchidae). Urbana: Illinois Natural History Survey Bull. Vol. **27**, Article 1, 83 pp., 27 figs., 27 tables.

Larson, Sten. 1957. The suborder Charadrii in arctic and boreal areas during the Tertiary and Pleistocene. A zoogeographic study. Acta Vertebratica, Vol. **1**, No. 1, 83 pp., figs. Stockholm: Nordiska Museet & Skansen, Almqvist & Wiksell. 15 Sw. kr.

Long Island Biological Association. 1957. Population Studies: Animal ecology and demography. (Symposium) Cold Spring Harbor Symposia on Quantitative Biology Vol. **22**, xiv + 437 pp., figs. & tables. $8.00. Cold Spring Harbor, N. Y.: The Biological Laboratory.

Lutz, R. J. & A. C. Cline. 1956. Results of the first thirty years of experimentation in silviculture in the Harvard Forest, 1908-1938. II. Natural reproduction methods in white pine-hemlock stands on light, sandy soils. Petersham, Mass.: Harvard Forest Bull. No. **27**, 70 pp., 22 figs., tables. $0.50.

McCabe, Thomas T. & Barbara D. Blanchard. 1950. Three species of Peromyscus. Santa Barbara, Calif.: Rood Associates. v + 136 pp., figs. & tables. $2.00.

Martin, Alex C., Ray C. Erickson, & John H. Steenis. 1957. Improving duck marshes by weed control. U. S. Dept. of Interior, Fish and Wildlife Service, Circular **19**—revised. 60 pp., figs. $0.25.

Mason, Herbert L. 1957. A flora of the marshes of California. Berkeley and Los Angeles: University of California Press. viii + 878 pp., 367 figs., taxonomic keys. $10.00.

Meyer, Arthur B. & F. H. Eyre. 1958. Forestry terminology. A glossary of technical terms used in forestry. 3rd ed. Washington: Society of American Foresters. v + 97 pp. $3.50.

Mitchell, Margaret H. 1957. Observations on birds of southeastern Brazil. Toronto: University of Toronto Press. 258 pp., figs. $4.50 paper, $5.50 cloth.

Müller, Andreas von. 1956. Über die Bodenwasser-Bewegung unter einigen Grünland-Gesellschaften des mittleren Wesertales und seiner Randgebeite. Angewandte Pflanzensoziologie [Stolzenau/Weser] **12**: 1-85, 55 figs., 22 tables. DM 14,80.

Nuttonson, M. Y. 1957. Barley-climate relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of barley. Washington: American Institute of Crop Ecology. vi + 280 pp., 17 figs., 125 charts, 127 tables.

Nuttonson, M. Y. 1958. Rye-climate relationships and the use of phenology in ascertaining the thermal and photo-thermal requirements of rye. Washington: American Institute of Crop Ecology. v + 219 pp., 17 figs., 87 charts, 87 tables.

Olson, Everett C. & Robert L. Miller. 1958. Morphological integration. Chicago: University of Chicago Press; London: Cambridge University Press. xv + 317 pp., 81 figs., 111 tables. $10.00.

Pettingill, Olin Sewall, Jr. 1956. A laboratory and field manual of ornithology. 3rd ed. Minneapolis: Burgess Publishing Co. viii + 379 pp., figs. and taxonomic keys.

Piveteau, Jean. 1957. Traité de paléontologie. Tome VII. Vers la forme humaine, le problème biologique de l'Homme, les étapes de l'intelligence. Primates—Paléontologie Humaine. Paris: Masson et Cie. 676 pp., 639 figs., 8 plates. 12.000 francs.

Rothstein, Jerome. 1958. Communication, organization, and science. With a foreword by C. A. Muses. Indian Hills, Colo.: Falcon's Wing Press. xcvi + 110 pp. $3.50.

Royce, William F. 1957. Observations on the spearfishes of the central Pacific. U. S. Dept. of Interior, Fish and Wildlife Service, Fishery Bull., Vol. **57**, No. 124, pp. 497-554, 27 figs., 11 tables. $0.40.

Rudnick, Dorothea (editor). 1957. Rhythmic and synthetic processes in growth. 15th Symposium of the Society for the Study of Development and Growth. Princeton: Princeton University Press. 217 pp., figs. $7.50.

Scheffer, Victor B. 1958. Seals, sea lions, and walruses. A review of the Pinnipedia. Stanford: Stanford University Press; London; Oxford University Press. x + 179 pp., 15 figs., 32 plates, 3 tables. $5.00.

Scott John Paul. 1958. Animal behavior. Chicago: University of Chicago Press. xi + 281 pp., 33 figs. 5.00.

Sears, Paul B. 1957. The ecology of man. Eugene: Oregon State System of Higher Education, Condon Lectures. 61 pp., 15 figs. $1.00.

Shaw, Samuel P. & C. Gordon Fredine. 1956. Wetlands of the United States. Their extent and their value to waterfowl and other wildlife. U. S. Dept. of Interior, Fish and Wildlife Service, Circular 39, iv + 67 pp., 33 figs., 8 tables, maps.

Sörlin, Anton. 1957. Växterna och människan. [Plants and man]. Stockholm: Lars Hökerbergs Bokförlag. 372 pp., 111 figs.

Stakman, E. C. & J. George Harrar. 1957. Principles of plant pathology. New York: Ronald Press Co. xi + 581 pp., figs. and tables. $8.00.

Stickel, Lucille F. 1957. Wildlife abstracts 1952-55. A bibliography and index of the abstracts in Wildlife Review numbers 67-83. U. S. Dept. of Interior, Fish and Wildlife Service. xxii + 331 pp.. $2.00.

Stout, Benjamin, B. 1952. Species distribution and soils in the Harvard Forest. Petersham, Mass.: Harvard Forest Bull. No. **24**: 1-29, 6 figs., 1 table. $0.25.

Stout, Benjamin B. 1956. Studies of the root systems of deciduous trees. Cambridge, Mass.: Harvard University, Black Rock Forest Bull. No. **15**: 1-45, figs. $0.50.

Thompson, Seton H. 1957. Alaska fishery and fur-seal industries, 1955. U. S. Dept. of Interior, Fish and Wildlife Service, Statistical Digest No. **40**, iv + 85 pp., 8 figs., 31 tables. $0.40.

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